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# Changes in the Great Smoky Mountains Fraser Fir Forest (1990-2000)

Report to the Great Smoky Mountains
National Park
October 2004

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## 1. SUMMARY

The southern Appalachian red spruce (*Picea rubens* Sarg.)-Fraser fir (*Abies fraseri* (Pursh) Poir.) forest is found on only seven high elevation areas in the southern Appalachian mountains. This relict ecosystem has been impacted by a number of environmental stresses including the infestation of fir by an exotic insect, the balsam woolly adelgid (*Adelges piceae* Ratz. Homoptera: Adelgidae). In 1990 a study was initiated in the Great Smoky Mountains National Park (GSMNP) to monitor changes in the overstory and understory of spruce-fir stands. Thirty-six 20x20 meter (m) permanent plots were established on five mountain peaks in the park. These plots were sampled again in 2000-01. Comparison to historical data indicates that from the late 1940s to 1990-91 live fir basal area and density decreased by 6.64 $m^2$/ha and 228 stems/ha respectively. Red spruce basal area decreased by 7.24 $m^2$/ha during this time, probably due to "thinning shock" created from exposure to wind, light, and temperature fluctuations. From 1990-2000 live overstory (≥5 cm dbh) fir density increased by 156 stems/ha. However, this cohort remained sparse compared to the late 1940s. Despite a heavily impacted overstory, mortality rates of all species were reduced since the late 1980s. The sapling (≥1.37 m tall, <5 cm dbh (diameter at breast height;1.37 m) Fraser fir, red spruce, and mountain-ash (*Sorbus americana* Marsh.) increased in density since 1990-91 illustrating a positive response to increased available light following infestation. Spruce and fir seedling (<1.37 m tall) density decreased as a result of competition for space from the sapling layer. The mean ages of the fir saplings were lower in 2000 than in 1990-91 suggesting a faster growing cohort. If adelgid populations do not stabilize and

Fraser fir does not develop a resistance, this cohort could be in jeopardy once it reaches maturity. Provided it lives long enough to produce viable seed it will become a two-aged forest never reaching the "old growth" uneven-aged structure that existed prior to infestation. Other possibilities are that the adelgid populations could stabilize or the fir could develop a resistance to the insect. In this case the forest could potentially reach an "old growth" uneven-aged structure similar to which existed before the introduction of the adelgid.

## 1. INTRODUCTION

The unique glacial relict spruce-fir ecosystem, of the southern Appalachians, are found only on seven high elevation mountain areas in North Carolina, Tennessee, and southwestern Virginia (Oosting and Billings 1951; Ramseur 1960). The spruce-fir reaches its maximum development at altitudes of about 1,830 m where spruce and fir comprise 95% or more of the canopy (Ramseur 1960). Red spruce tends to grow taller and often lives more than 300 years while fir reaches a maximum age around 150 years (Korstian 1937; Oosting and Billings 1951).

Large tracts of red spruce forests in the southern Appalachians were logged for their high commercial value as lumber and pulpwood at the turn of the 20$^{th}$ century (Korstian 1937; Pyle 1984). Fires often followed and eventually led to the destruction of an estimated 50% to 90% of the spruce-fir forest in the Southeast (Korstian 1937; Pyle and Schafale 1988).

In 1957, the balsam woolly adelgid, a serious pest to all true firs, was first detected in the southern Appalachians when it was found on Mt Mitchell in western North Carolina (Speers 1958; McCambridge 1958). It was thought to have arrived on imported nursery stock of European silver fir (*Abies alba* Miller) (Kotinsky 1916; Amman 1962). In 1963, it was found on Mt. Sterling in the GSMNP (Ciesla et al. 1963). The adelgid is currently located throughout the native range of Fraser fir causing high amounts of mortality impacting the ecosystem (Ciesla et al. 1963; Amman and Speers 1965; Hay et al. 1976; Eagar 1978; DeSelm and Bonner 1984; Zedaker et al. 1988; Dull et al. 1988; Busing and Clebsch 1988; Nicholas et al. 1992a; Smith and Nicholas 1995; Smith 1997).

Fraser fir is not the only overstory species suffering from the adelgid. Spruce, which characteristically has a shallow root system (Crandall 1958), is affected by the increased wind exposure due to the death of neighboring surrounding fir as a form of "thinning shock" (Nicholas et al. 1992b).

In addition to "thinning shock" the spruce has been suggested to be suffering from a recent decline in vigor since the 1960s (Mclaughlin et al. 1990). This decline has been attributed to synchronic large-scale disturbances, which initiated changes in stand dynamics (Hornbeck et al. 1986; Reams and Huso 1990; Van Deusen et al. 1991) and high amounts of atmospheric deposition (acid rain, ozone, etc.) (Johnson 1991).

Another canopy associate, mountain-ash (*Sorbus americana* Marsh.), has also recently suffered from an exotic pest. Between 1985 and 1989 Nicholas (1992) found 11.7 percent annual mortality of mountain-ash in three southern Appalachian spruce-fir forests. Nicholas (1992) suspected the exotic mountain-ash sawfly (*Pristiphora geniculata* Hartig,) was a dominant factor in the high mortality of this species.

Current warmer climate trends could also have a negative impact on this ecosystem. Delcourt and Delcourt (1998) suggest that a warmer, drier climate could force the red spruce-Fraser fir ecosystem to higher elevations. Since the mountains in the southeast are all under 2,100 m tall and the mean global temperature is estimated to increase by 1.5° to 4.5° C over the next century (Root and Schneider 1993) this poses a serious threat.

Despite recent disturbances in the overstory during the past century, studies indicate a positive response in understory fir to overstory deterioration (DeSelm and Bonner 1984; Witter and Ragenovich 1986; Witter 1988; Nicholas et al. 1992a; Smith 1997). In fact,

DeSelm and Boner (1984) reported large densities of fir saplings being recruited into the overstory within 11-20 years of initial infestation. According to Smith (1997) these new recruits grow at an accelerated rate as a result of the reduced overstory. In order for this young cohort to maintain itself, however, seedlings and saplings must live to seed bearing age (approximately 15 years) and be able to produce viable seed (Busing et al. 1988; Pauley and Clebsch 1990; Nicholas et al. 1992b).

Red spruce-Fraser fir forests hold both tangible and aesthetic values. The high elevations are popular tourist destinations. A regional Christmas tree industry depends on a large and genetically viable seed stock of Fraser fir for local sources. This ecosystem is located at the headwaters of many watersheds in the region, the loss of overstory fir could have serious impacts on water quality and habitat downstream (Pyle 1984). Of the 142 vascular plant species that occur in the Great Smoky Mountains spruce-fir forests, 16 are endemic (White and Renfro 1984; Rock 2002). This forest provides habitat for federally listed endangered animal species such as the northern flying squirrel (*Glaucomys sabrinus* Shaw) (Weigl et al. 1992), and the endemic spruce-fir moss spider (*Microhexura montivaga* Crosby and Bishop) (USFWS 1995). These forests have high importance in biodiversity, an issue of global concern. Alterations in the structure of this forest could have some negative effects on biodiversity (Bonner 1979; Smith 1984; Mathews and Echternaccht 1984; DeSelm and Bonner 1984; Hall 1989; Nicholas et al. 1992b; USFWS 1995; Rabenold et al. 1998).

# 2. LITERATURE REVIEW

## 2.1. Biology of the Great Smoky Mountains Spruce-Fir Forests

This section includes a discussion of abundance and distribution of vegetation typically found in the spruce-fir ecosystem and forest dynamics, including disturbance patterns and gap dynamics.

### 2.1.1. Abundance and Distribution of Vegetation

The red spruce-Fraser fir community typically ranges from 1,500 to 2,000 m in elevation in the southern Appalachians. It is most prevalent in the Great Smoky Mountains (75% of the fir in the Southeast) where it may extend down to 1,370 m (Oosting and Billings 1951; Whittaker 1956). The southern Appalachians (35-37° N) have 10 mountainous areas separated by gaps that surpass 1,680 m, the average elevation for the transition from deciduous forests to spruce-fir at this latitude (Ramseur 1960). However, well developed stands occur in only seven high mountain areas (>1,750 m): Mount Rogers, Virginia; Grandfather Mountain, North Carolina; Roan Mountain, Tennessee; the Black Mountains, North Carolina; the Balsam Mountains, North Carolina; the Plott Balsam Mountains, North Carolina; and the Great Smoky Mountains, Tennessee and North Carolina. The three remaining mountainous areas over 1,680 m, (Whitetop, Virginia; the Great Craggy Mountains, North Carolina; and Mount Pisgah, North Carolina) have only spruce stands. Of these three areas, Whitetop is the only area with a well developed population of spruce (Ramseur 1960).

Fraser fir is one of 16 endemic species of the high elevation southern Appalachians while the range of red spruce extends northeast to Canada (White and Renfro 1984).

Spruce thrives in the southern Appalachians due to higher moisture availability (Murphy 1917; Westveld 1930; Dana 1930).

According to Busing et al. (1993) elevation has the most influence on the composition of the tree stratum in the southern spruce-fir ecosystem. The elevation gradient of dominant spruce stands ranges from 1,370 to 1,675 m (Whittaker 1956). Spruce and fir codominate from 1,675 m to 1,890 m. In these mixed stands Oosting and Billings (1951) noted that on average fir was three to five times as abundant as spruce. Busing et al. (1993) and Smith (1997) found that spruce dominates more on the steeper slopes where there is less exposure to wind. Above 1,890 m Fraser fir, which has a greater tolerance for cold and wind, increases in relative dominance and forms almost pure stands on high summits and ridges (Whittaker 1956; Dehayes et al. 1990; Busing et al. 1993; Smith 1997). Cain (1935) observed smaller even-aged "pole stands" of fir in many of the higher elevation areas.

In the higher elevation forests the most abundant deciduous tree is mountain-ash (*Sorbus americana* Marsh.) (Oosting and Billings 1951; Whittaker 1956; Ramseur 1960). At the mid to lower elevations yellow birch (*Betula allegheniensis* Britton) becomes a prevalent canopy tree (Oosting and Billings 1951; Whittaker 1956; Ramseur 1960). Pin cherry (*Prunus pennsylvanica* L.f.), is occasionally found as a canopy tree, usually originating from a minor disturbance (Ramseur 1960). American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow buckeye (*Aesculus octandra* Marsh.), mountain maple (*Acer spicatum* Lam.), striped maple (*Acer pensylvanicum* L.), red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.),

serviceberry (*Amelanchier arborea* var. *lavis* (Wieg.) Ahles.), mountain silverbell (*Halesia monticola* (Rehd.) Sarg.), northern red oak (Quercus rubra (L.)) and sugar maple (*Acer saccharum* Marsh.), may be encountered in the lower spruce-fir elevations (Korstian 1937; Oosting and Billings 1951; Whittaker 1956; Crandall 1958; Ramseur 1960). Common shrubby plants in the understory include witch-hobble (*Viburnum alnifolium* Marsh.), bearberry (*Vaccinium erythrocarpum* Michx.), rhododendron (*Rhododendron spp.*), highbush blueberry (*Vaccinium corymbossum* (L.)), and mountain laurel (*Kalmia latifolia* (L.)) which form dense layers on more xeric ridges (Cain 1935; Oosting and Billings 1951; Ramseur 1960). Elderberry (*Sambucus pubens* Michx.) and blackberry (*Rubus canadensis* L.) occur in many canopy gaps (Ramseur 1960).

High densities of mosses, liverworts, and lichens cover the shallow, rocky, poorly drained, and highly acidic soil (Cain 1935). The dominant herbaceous plants are the ferns (Ramseur 1960). Norris (1964) documented 203 species of bryophytes; 36 of which grow on live fir boles. Of these 36 species there are six that are nearly restricted to fir (Smith 1984). Choberka (1974) found 30 species of mosses and liverworts that depended on decaying fir logs for habitat and survival.

### 2.1.2. Stand Dynamics and Natural Disturbances

Fraser fir typically lives to 150 years (Korstian 1937), rarely growing greater than 24 m tall and 61 cm dbh (Beck 1990). Seed production begins at about 15 years of age and good crops occur every other year (Beck 1990). Fir relies heavily on advanced regeneration and can remain stagnant in the understory for over 40 years (Beck 1990).

Red spruce, which can live longer than 300 years (Korstian 1937), begins to produce heavy seed crops around age 30 (Korstian 1937) at three to eight year intervals (Blum 1990). Once established, spruce can remain in the understory for over 50 years (Oosting and Billings 1951). In the Southern Appalachians, overstory spruce attains heights of over 30 m (Korstian 1937).

The shade tolerant yellow birch produces good seed crops in 2 to 3 year intervals starting at approximately age 40 (Erdmann 1990). Yellow birch typically lives longer than 300 years and grows taller than 30 m (Erdmann 1990).

Mountain-ash rarely reaches the canopy (Ramseur 1960) growing 3-10 m high (Dirr 1998). The number of stems of this shade intolerant shrubby species is sparse relative to spruce and fir (Oosting and Billings 1951).

Small canopy gaps tend to dominate the natural disturbance regime of old growth spruce-fir forests in the Great Smoky Mountains (White et al. 1985). According to White et al. (1985) natural disturbances in the spruce-fir ecosystem fall into three main categories: (relatively unimportant) lightning fires, (locally important) debris avalanches (Bogucki 1970), and (very important) windthrows. There are two types of wind disturbances: large blowdowns (>200 $m^2$) and smaller windfall gaps (<200 $m^2$). White et al. (1985) found that in old growth spruce-fir forests the smaller windfall gaps were the most widely distributed. In the higher elevation pure fir forests patches of multiple blowdowns were more prevalent. Fire was of less importance as a disturbance factor because fuel moisture and humidity is high and lightning is usually accompanied by prolonged rainfall (Harmon 1981).

Gaps created from falling spruce due to wind-throw, debris slides, and ice/snow damage is a natural characteristic of this ecosystem, and may have little long term consequences as long as there is sufficient regeneration (Nicholas et al. 1992b). According to Crandall (1958) spruce roots do not penetrate into the soil more than 46 to 61 cm with the larger roots spreading only three to five meters from the base of the tree. This makes spruce more susceptible to wind throw than fir. Moore (1917) stated that fir roots are more deeply rooted and less branched. This causes them to break off more frequently rather than be uprooted (Crandall 1958).

## 2.2. History of the Great Smoky Mountains Spruce-Fir Forests

This section covers the history of the Great Smoky Mountains spruce-fir forests, including fir migration to its northerly and high elevation extent in response to the global climate warming, and evolution of northerly and southerly populations into balsam fir (*Abies balsamea* (L.) Mill.), and Fraser fir. Anthropogenic disturbances including human caused fire, and more recent intensive logging operations and air pollution are covered.

### 2.2.1. Paleoecology and Evolution of Fraser Fir

Approximately 18,000 YRBP (Years Before Present) to 12,500 YRBP (the late Wisconsinan full-glacial period) the spruce-fir occupied an area eastward from Missouri across Tennessee and into the Carolinas (Delcourt and Delcourt 1984). At this time fir made up 10% of the forests in Tennessee and North Carolina at 36° to 37° N latitude (Delcourt and Delcourt 1984). As the Laurentide Ice Sheet receded (approximately 14,000 YRBP) the spruce-fir forests migrated northwards and upwards to seek sanctuary

from the warmer temperatures of the Xerothermic period (Whittaker 1956; Delcourt and Delcourt 1984). The ecotones between alpine, boreal, and temperate ecosystems changed extensively in the southern Appalachians during this time, because of the passage of critical thresholds of temperature and changing disturbance regimes (Delcourt and Delcourt 1984). During this time the spruce-fir forests on the peaks below 1,707-1,768 m were extirpated and northern populations of balsam fir were probably separated from Fraser fir (Delcourt and Delcourt 1984). When the climate cooled again, the spruce-fir forests migrated to elevations as low as 1,370 m (Whittaker 1956). However, the forests did not migrate to some of the peaks above 1,370 m, such as Whitetop in southwestern Virginia, because of the barriers caused by low elevations (Rheinhardt 1984).

This population bottleneck created a smaller genetic diversity of subpopulations of Fraser fir, and resulted in a higher genetic diversity of balsam fir, which has a larger range (Diebel and Feret 1991).

After the end of the last ice-age fir evolved into three closely related taxa in the eastern United States: (1) balsam fir (*A. balsamea* (L.) Mill.) in the northern Appalachians, (2) intermediate fir (*A. balsamea* var. *phanerolepis* Fern.), in high elevations in Virginia, and West Virginia, (3) Fraser fir (*Abies fraseri* (Pursh) Poir.) in southwest Virginia, western North Carolina, and eastern Tennessee at elevations above 1,300 m (Liu 1971). The three taxa differ in the relative cone bracts to the cone scale lengths, number of leaf hypodermal cells, and geographic location (Myers and Bormann 1963; Robinson and Thor 1969; Liu 1971; Thor and Barnett 1974). Fraser fir has long exerted and reflexed bracts, while balsam fir has bracts which are mostly included. *A.*

*balsamaea* var. *phanerolepis* is intermediate between the two, and has slightly exerted bracts that are occasionally reflexed. Fraser fir has a much higher number of leaf hypodermal cells than either of the other varieties (Robinson and Thor 1969).

There are two different hypotheses which attempt to explain the genetic separation of the three taxa. One theory suggests that *A. balsamea* var. *phanerolepis* could be a hybrid of the balsam and Fraser fir (Fulling 1936; Ramseur 1961; Liu 1971) which existed in the same geographical area in response to environmental changes during the Pleistocene age (1.6 million years before present) (Jacobs et al. 1984). The second, more popular, hypothesis is that all three taxa evolved from a single population of fir which was separated during the Pleistocene (Mark 1958; Robinson and Thor 1969; Clarkson and Fairbrothers 1970; Zarvin 1972; Thor and Barnett 1974).

Robinson and Thor (1969) tested the theory of hybrid origin of intermediate fir and rejected their hypothesis. They observed foliage, seed, and cone characteristics and concluded that the ranges and standard errors of these characteristics among the intermediate populations were far too small than would be expected to support the hybrid theory. The same conclusion was reached by Thor and Barnett (1974), who analyzed wood and monoterpenes. They further proposed that there should be only one species of *Abies*, in eastern North America, with three varieties: (1) *A. balsamae* var. *balsamaea* (2) *A. balsamae* var. *phanerolepis* and (3) *A. balsamae* var. *fraseri* (Thor and Barnett 1974; Jacobs et al. 1984). Jaccobs et al. (1984) electrophoretically analyzed twenty gene loci from twelve populations representing all three taxa. They found that distances between the three taxa fall within the expected range of a single species. They further supported

the idea that *A. fraseri* is an adaptive extreme of *A. balsamea* that was separated during the Wisconsinan, and evolved after climate warming.

Several studies have examined the genetic variations of Fraser fir. Li et al. (1988) observed that fir seedlings from lower elevation peaks grew higher than those of greater elevation. They also observed that seedlings from more southerly areas showed better height performance. Diebel and Feret (1991) however, noticed very little microgeographic differentiation when analyzing thirteen isozyme loci on Mt. Rogers. They suggested that there is much less genetic differentiation in Fraser fir than balsam fir. However most empirical studies of forest trees have shown that isozymes are not traits subjected to intense selection pressures (Falkenhagen 1985). Nonetheless, Auckland et al. (2001) reported there were no significant differences in mean DNA content among six isolated Fraser fir populations.

### 2.2.2. Anthropogenic Disturbance

According to Dickens (1976) humans have inhabited the southern Appalachians for more than 12,000 years. However, the Great Smoky Mountains spruce-fir forest was likely visited very seldom by humans before the construction of logging railroads because of its inaccessibility. In fact, the only Native American artifacts found to date in the Great Smoky Mountains spruce-fir forests were along the old trail at Indian Gap (Pyle and Schafale 1988). By the time Euro-American settlers made contact with the Cherokee, human set fire was the largest landscape influence in the southern Appalachians (Goodwin 1977). However this had little effect on the spruce-fir forest. Occasionally, fire spread into the spruce-fir forests from lower elevation deciduous forests, or were

accidentally set by hunters. Livestock grazing occasionally occurred in this area, but overall, the change in the landscape in the lower elevation deciduous forests were much more significant.

The increased demand for valuable red spruce timber pushed the logging companies south to exploit the unlogged southern Appalachians spruce forests. Its usefulness as sawtimber and pulpwood led to the demise of a large portion of its former expanse (Korstian 1937). The logging operations of spruce in the southern Appalachians began in 1905 on Mount Rogers and quickly moved south. The Great Smoky Mountains were cut last due to their inaccessibility (Pyle and Schafale 1988). The most common method used was to remove spruce logs by railroad in combination with ground or overhead steam skidding or animal skidding. Korstian (1937) observed that steam skidding caused more damage to the residual stand than any other method. This technique left uprooted seedlings and slash, which covered the seedlings that survived. Another practice which caused great damage to the understory was fluming, a technique used to remove logs by rolling them down steep slopes.

Following the logging, the land was subjected to high levels of sunlight that desiccated the organic soil and dried out the slash, creating a highly flammable area. Fire resulted in denuding the land and, in turn, caused increased erosion. Blackberry colonizers, followed by pin cherry and yellow birch inhibited the germination of spruce and fir (Korstian 1937; Pyle 1984; Pauley and Clebsch 1990). On certain burn areas Pyle and Schafale (1988) observed that areas that previously supported spruce-fir forest now sustained open stands of yellow birch, fire cherry, shrubs (especially blackberry), and

grasses. According to Hayes (2002) the lower elevational extent of spruce-fir was increased due to poor regeneration on these disturbed areas. Because of its inaccessibility, the negative effects of logging affected the spruce-fir forests the least of any area in the Great Smoky Mountains. Likewise, Pyle (1984) found that as much as 13,370 ha of the original 17,910 ha of spruce-fir forests in the GSMNP were left untouched by the effects of logging and burning.

Logging and fire were profound threats to the spruce-fir forest. However not all threats are as well defined. Bruck (1984), Bruck and Robarge (1984), Adams et al. (1985), and Cook (1988) reported reductions in radial growth of some high elevation southern and mid-Appalachian red spruce trees during the 1960s-1980s. Current studies however contradict that southern red spruce is suffering from growth decline (Cook and Zedaker 1992; Goelz et al. 1999) Goelz et al. (1999), for example, found no reduction in growth rings in red spruce on Mt. Rogers, and Mt. Mitchell.

The reason for the supposed decline in the red spruce population since the 1960s can be explained by two hypotheses, which are not mutually exclusive: (1) synchronic large-scale disturbances have initiated changes in stand dynamics in the red spruce ecosystem and (2) normal growth processes have been altered by high amounts of atmospheric deposition (acid rain, ozone, etc.) (Johnson and Siccama 1983; Bruck 1984; Bruck and Robarge 1984; Adams et al. 1985; Mclaughlin et al. 1987; Cook 1988; Peart et al. 1992; Shepard et al. 1995).

Zedaker et al. (1987), McLaughlin et al. (1987), and Peart et al. (1992) conclude that the first hypothesis was more accurate, and that there was little evidence to suggest that

there is a link between pollution and stand conditions. They suggested that if there was a decrease in incremental growth it had more to do with other factors such as drought, or exposure to wind and ice resulting from the death of nearby fir (Nicholas et al. 1992a).

Bruck (1984), Bruck and Robarge (1984), Adams et al. (1985), McLaughlin et al. (1991), McLaughlin and Tojoelker (1992), McLaughlin et al. (1993), and Shepard et al. (1995) offer evidence to support the second hypothesis, i.e. a link between acidic deposition and the decline of red spruce.

Both northern and southern spruce-fir forests receive high rates of acidic deposition from rainfall and clouds. In fact the southern Appalachian spruce-fir forests receive among the highest loadings of nitrogen and sulfur measured in North America (Johnson and Lindberg 1992). Saxena and Lin (1990) supported this claim when reporting that Mt. Mitchell, North Carolina, was exposed to acidic fogs 70% of the days in a year, and 35% of the time.

This large amount of acidic deposition has been shown to reduce calcium and magnesium availability, important nutrients in regulating red spruce health. For example, in the northeast, acidic deposition has been known to reduce cold hardiness of red spruce (Dehayes et al. 1990). In Europe, German scientists have hypothesized that foliar leaching of calcium and magnesium caused by acidic deposition is one of the major contributors to certain diseases in closely related Norway spruce (*Picea abies* (L.) Karsten) (Zoettl and Huettl 1986; Rehfuess and Bosch 1986; Bosch et al. 1986).

It is possible that both spruce and Fraser fir are negatively affected by atmospheric pollutants (Eagar 1984; Hain and Arthur 1985; Shepard et al. 1995). According to Hain

and Arthur (1985) atmospheric pollution may reduce Fraser fir's host susceptibility to balsam woolly adelgid attack. Hollingsworth and Hain (1991), and Shepard et al. (1995) suggest that pollution induced deficiencies of soil nutrients, such as calcium, increase Fraser fir's susceptibility to the adelgid by leaching basic cations from the soil. This lack of calcium in the tree reduces its wound response caused by the adelgid.

However, the idea that atmospheric deposition may predispose Fraser fir to mortality caused by the adelgid is subject to much speculation (Nicholas et al. 1992a; Lee et al. 1997). Mitchell (1966) offers strong evidence to discredit this idea observing that in the relatively pristine Pacific Northwest the balsam woolly adelgid causes significant mortality.

Another formidable threat to this ecosystem is possible climate warming. Delcourt and Delcourt (1998) suggest that a warmer, drier climate could force the red spruce-Fraser fir ecosystem to higher elevations. Since the mountains in the southeast are all under 2,100 m tall and the mean global temperature is estimated to increase by 1.5° to 4.5° C over the next century (Root and Schneider 1993), this poses a serious threat.

## 2.3. Balsam Woolly Adelgid and Current Status of the Red Spruce-Fraser Fir Forests

The following section describes the life history of the balsam woolly adelgid and its physiological impacts on Fraser fir. Also discussed are the impacts it has on the community and ecosystem, followed by fir regeneration and future prospects.

### 2.3.1. Adelgid Biology and Spread

The balsam woolly adelgid is a serious pest to all true firs, and is responsible for high levels of tree mortality in North America and Canada (Pope 1958; Amman 1962). It is native to Europe where it feeds on European silver fir causing only slight damage (Eagar 1984). It was first detected in North America in 1908 (Kotinsky 1916) but was not detected in the Southern Appalachians until 1957 when it was found on Mt Mitchell (Eagar 1984). The most accepted hypothesis of its introduction to the United States is that it arrived on imported nursery stock of silver fir (Kotinsky 1916).

The first adelgid survey of Mt. Mitchell, North Carolina in 1958 showed that 11,000 trees had been killed by the adelgid and the infestation covered the entire spruce-fir stand in the Black Mountains (Ciesla et al. 1963). In 1960, an aerial survey estimated that 200,000 trees had been killed in the Mt. Mitchell area. This represented about 7% of the fir of the entire 5,536 hectare area (Amman and Speers 1965). Since then the infestation spread to other areas in the Appalachian mountains causing high amounts of mortality (Amman and Speers 1965).

The adelgid was first detected in the Great Smoky Mountains in 1963 (Amman and Speers 1965). One mile north of Mt. Sterling a stand of 45 adelgid killed trees was the first observation of balsam woolly adelgid in the park (Ciesla et al. 1963). In an effort to control this outbreak the GSMNP performed sanitation cuttings on infested trees on Mt. Sterling in September of 1963 (Eagar 1978). However the adelgid continued to spread and the cuttings were aborted. It was monitored in the Park as it spread to Cataloochee Knob, and then to the southeast slope of Mt. Guyot (Ciesla et al. 1963; Lambert and

Ciesla 1966; Lambert and Ciesla 1967). From there, the outbreak spread from Mt. Guyot to Mt. LeConte and Clingmans Dome (Eagar 1978). Currently, the adelgid is located throughout the native range of Fraser fir.

Depending on the climatic conditions, the balsam woolly adelgid (most of which are female in North America (Amman and Speers 1965)) can have two or more generations per year (Marchal 1913; Brower 1947; Brower 1947; Balch 1952; Balch 1952; Varty 1956; Karafiat and Franz 1956; Karafiat and Franz 1956; Varty 1956; Johnson and Wright 1957; Johnson and Wright 1957; Tunnock and Rudinsky 1959; Tunnock and Rudinsky 1959; Tunnock and Rudinsky 1959). However Amman and Speers (1965) noted that it was possible for a female to produce as many as four generations per year in warm and moist conditions as found in the Southeast.

The female adelgid can lay as many as 100 eggs which hatch into small first-instar nymphs (Amman and Speers 1965). This is the only motile form of the insects (Amman 1962). During this stage they are dispersed by wind, birds, or other natural causes (Amman and Speers 1965).

Eagar (1978, 1984) proposed that stands with large spruce protruding above the canopy create a filter effect which intercepts the wind disseminated adelgids. The adelgids are then able to fall or crawl to the fir boles below. Smith (1997) confirmed this idea by noting that there were high numbers of large spruce where there were high numbers of dead understory fir.

After the insect locates a suitable spot on the fir tree it inserts its stylet and enters diapause for two to eight weeks in the summer before development begins (Amman

1962; Ciesla et al. 1963). It then overwinters as a first instar nymph while passing through three nymphal instars, and becomes a wingless parthenogentic adult about 1 mm in length (Amman 1962; Ciesla et al. 1963). Within a few days the adelgid begins laying eggs (Ciesla et al. 1963).

The adelgid-infested trees react quickly to the attack with two responses: (1) rapid radial growth of the trunk and branches resulting in poor conductance caused by the formation of compression like wood (commonly called "rotholz" or redwood (Ciesla et al. 1963), and (2) gouting of twigs and buds which prevents new foliage growth (Amman 1962; Amman and Speers 1965). Both of these are caused by salivary injections from the adelgid (Balch 1952).

The saliva contains a growth-stimulating substance, increasing cell division in the cambium and causing the production of trachieds with thick cell walls, and dark, hard, brittle wood. (Ciesla et al. 1963; Balch et al. 1964). This may increase heartwood formation (Hollingsworth and Hain 1991), which interferes with conduction (Amman and Talerico 1967).

Stem infestation is the predominant form of adelgid attack in Fraser fir (Amman and Talerico 1967). The first sign of a stem attack is needle color change to yellow-green, then red, and then brown (Ciesla et al. 1965). A tree may die within two to five years depending on the degree of infestation (Amman and Speers 1965; Amman and Talerico 1967).

Young vigorous fir saplings in even-aged pure stands are not as susceptible to the insect because of their tight, smooth, grey bark (Eagar 1984). When the saplings grow

older however they develop bark fissures which allow the adelgid easier access to the pheloderm (Eagar 1985). Eagar (1984) and (1985) found that the surfaces of open grown fir tees were not suitable for adelgid feeding until around 25 years old or 4 cm dbh.

Although smooth-barked young trees are able to avoid stem attack, they may suffer from crown infestations which result in gouting of twigs. This causes nodal swelling, shoot thickening, and tip inhibition; defoliation, dieback, and/or stem taper (Amman and Talerico 1967; Eagar 1984). Crown infestation of the understory is rare in Fraser fir and only occurs under a heavily infested overstory. In this situation recovery is possible if the young tree is not seriously damaged by the time the older trees die and the infestation stops (Eagar 1984).

Although the adelgid attacks all firs, certain species are more resistant than others. Hollingsworth and Hain (1992) observed the responses of Fraser, balsam, and European silver fir to the balsam woolly adelgid. Balsam and silver fir responded by forming an outer bark layer which resisted the adelgid by forming a physical barrier. This reduced the formation of rotholz. Hollingsworth and Hain (1992) suggested that this is the reason that Fraser fir is more susceptible to the adelgid. They further noted that the fir on Mt. Rogers produced a thicker outer bark layer than that of Mt. Mitchell, concluding that the Mt. Rogers fir had a special enhanced resistance to the insect. Likewise, several studies have shown that northern Fraser fir produces less rotholz than southern Fraser fir (Arthur and Hain 1985; Arthur and Hain 1987; Hollingsworth and Hain 1991; Hollingsworth and Hain 1992).

While mature fir is able to produce a protective outer bark layer, juvenile fir has a different mechanism of resistance. Past studies have shown that certain conifers produce monoterpenes in order to repel insects and reduce predation (Sturgeon 1979). According to Zhang (1994) juvabione, a juvenile hormone related compound (JRC) thought to inhibit the reproduction of adelgids (Puritch and Nijholt 1974), increased in Fraser fir with degree of infestation. However, Sutton et al. (1997) observed at Mt. Rogers and Roan Mountain that there was little difference in monoterpene concentration between infested and uninfested Fraser fir.

The balsam woolly adelgid is extremely resistant to climate-caused mortality (Eagar 1984). Warmer temperatures, in fact, increase their fecundity rate (Eagar 1984). Extremely cold temperatures limit reproduction in the northern populations, but have little effect in the southern Appalachians (Eagar 1984).

Amman (1970) observed that the most important factor affecting the adelgid population was the condition of the host tree. He also noted that native predators had little effect. Weather factors were found to cause large amounts of egg mortality, but had very little long term effect.

There have been very limited results with human control of the adelgid. Attempts were made in the 1960's to control the spread of the insect by cutting down infested trees in the Great Smoky Mountains (Ciesla et al. 1965). Unfortunately, this method proved ineffective because eggs and crawlers are easily detached from the fallen trees and dispersed by wind and likely increased the spread of the pest (Lambert and Ciesla 1966).

Another failed attempt at control was the use of a ⅛% benzene hexachloride water emulsion used for treatment in areas of high aesthetic and recreation value (Amman and Speers 1965; Ciesla et al. 1965). Aerial application was impractical because the entire bole of the tree had to be covered. Hence, the only trees that could be treated were those adjacent to the roadside where pump units were used to spray the boles (Amman and Speers 1965). The biggest drawback of lindane however was its persistence in the environment and contamination of the water table (Eagar 1984).

Another method of control is potassium oleate soap, which was applied annually to stands around the parking lot and trail to the observation tower at Clingmans Dome and currently to the roadside accessible fir on Balsam Mountain in the Great Smoky Mountains (Taylor 2002, personal communication). Treatments were started on both peaks in the mid 1980s and ended on Clingmans Dome in 1999. This alternative is less toxic and because it is made up of fatty acids it biodegrades at a faster rate (Eagar 1984). This method is also of limited effectiveness because of the inaccessibility of most stands of fir (Eagar 1984).

Experiments using biological control were tested on Mt. Mitchell between 1961 and 1965, when 15 species of predators from India and Pakistan were introduced (Amman and Speers 1971). The use of these predators proved unsuccessful because of an inability to adapt to the change in climate, and poor prey acceptances.

### 2.3.2. Community and Ecosystem Impacts

In 1946 Oostings and Billings sampled seven stands of spruce-fir in the GSMNP. This data is used as a benchmark for pre-adelgid infestation conditions in the Smoky

Mountains. Several studies showed that since 1946 there has been significant change in the overstory and understory.

Boner (1979) compared recently infested Great Smoky Mountain spruce-fir stands with spruce-fir stands in the Black Mountains of North Carolina where the adelgids had been present for up to twenty years. Although the elevations and site conditions varied with each site, he found that total overstory densities and basal areas and fir densities and basal areas decreased with time since initial infestation.

In 1988 Busing et. al. reported on changes in two .405 ha. old growth spruce-fir plots that were previously sampled before adelgid infestation. They quantified changes in stand composition, structure, and growth and found that overstory fir basal area had been reduced by 54% and 97% in the two plots (Busing et al. 1988).

Nicholas et al. (1992b) compared the basal area and density of 66 plots in the Great Smoky Mountains, in 1985 and 1986, with data from Oostings and Billings (1951). They found that in 1985 and 1986 the densities were only 8 and 62% respectively of those found in 1946.

Smith and Nicholas (1998) reported that nearly 70% of overstory fir (≥5 cm dbh) in the Great Smoky Mountains was standing dead in 1990-91. They suggested that the initial wave of adelgid mortality was virtually complete in the southern Appalachians by the early 1990s, based on observations of lower mean annual fir mortality rates than previously found in earlier research (Smith and Nicholas 1999).

Fraser fir is not the only overstory tree negatively affected by the balsam woolly adelgid. Although understory spruce have been shown to respond positively to thinning

(Zedaker et al. 1988; Reams and Van Deusen 1993), overstory spruce suffers from thinning shock due to the death of nearby fir (Nicholas et al. 1992a).

Busing and Pauley (1994) reported that mortality rates of overstory spruce trees were less than 2% per year after the loss of overstory fir from the canopy. However they further reported that uprooting or snapping due to wind accounted for 94% of the spruce mortality in previously infested stands (Busing and Pauley 1994). They compared this to Busing and Wu (1990) who found less than 60% of spruce death attributed to wind prior to adelgid infestation.

Bonner (1979) found that the most significant change in the spruce-fir forests following adelgid infestation were in the understory and ground cover strata. He noted that hobblebush and more so thornless blackberry showed significant increases in density with time since initial infestation. This was also noted by Busing et al. (1988) when they noted that thornless blackberry covered 25-50% of two .405 ha plots which prior to infestation had none. He suggested this was in response to the increased levels of light and temperature (Busing et al. 1988).

DeSelm and Boner (1984) found other species which increased in density with removal of the fir overstory; yellow birch, and mountain maple saplings, fire cherry, minnie-bush (*Menziesia pilosa* Michaux), round leaf gooseberry (*Ribes rotindafolium* Michaux), and red berried elder subsapling-shrub stems, and ground cover such as ferns and mosses.

The changes in ground cover of herbs and bryophytes after overstory mortality caused by the adelgid mirrors that of the response to a large blowdown. Boner (1979) found that

common wood-shamrock average cover decreased from 32% in the uninfested plots, to 6% in the plots that had been infested for 11-20 years. Likewise, moss cover decreased from 19% to 10%. Crandall (1958) reported a similar response when observing large blowdowns in the spruce-fir forest. She noted that in a stand on Clingmans Dome with high amounts of blowdowns, the wood-shamrock and mosses averaged less than 1% cover, herbs 57%, and ferns 60% cover. The undisturbed areas however averaged 38% cover by mosses, 50% by wood-shamrock, and 94% by ferns, but only 8% by herbs.

Mountain-ash usually responds positively to an increase in sunlight. However Nicholas (1992a) found high levels of mountain ash mortality in three southern Appalachian spruce-fir forests between 1985 and 1989. She hypothesized that the mountain ash sawfly (*Pristiphora geniculata* Hartig), probably was a major contributor (Nicholas et al. 1992a).

All of this mortality in the overstory will disrupt ecosystem processes, such as nutrient cycling, energy flow and disturbance regimes. Joslin et al. (1998) reported a possible decrease in soil organic matter as a result of enhanced decomposition rates caused by soil warming. This in combination with large amounts of dead fir wood could significantly increase the C/N ratio (Joslin et al. 1998; Rose 2000). This would increase carbon dioxide released into the atmosphere, and release large stores of nitrogen resulting in soil acidification, aluminum (Al) mobilization, and leaching of base cations (Joslin et al. 1998). Since the Great Smoky Mountain spruce-fir forests are located at the headwaters of 17 of 28 watersheds in the Park, this could have implications on other forest types (Pyle 1984).

### 2.3.3. Fraser Fir Regeneration and Future Prospects

The USDI Fish and Wildlife Service reviewed Fraser fir for possible listing as a threatened or endangered species in 1993. Currently it is not federally listed as endangered or as a candidate species

Although past studies show a decrease in overstory Fraser fir, the understory tends to respond with increased density and vigor (DeSelm and Bonner 1984; Witter and Ragenovich 1986; Witter 1988; Nicholas et al. 1992a; Smith 1997). Bonner (1979) noted that subsapling fir (≥0.6 m tall, ≤2.5 cm dbh) density increased with time since the death of the overstory. Smith (1997) made a similar observation. DeSelm and Boner (1984) reported large densities of saplings being recruited into the overstory class within 11-20 years of initial infestation. Pauley and Clebsh (1990) found fir seedling densities of 33,000 stems/ha on recently infested Mount Collins. Nicholas et al. (1992a) observed in the Great Smoky Mountains that between 1985 and 1989 spruce and fir seedling densities remained in a stable reverse J-shaped curve.

For the continued survival of the Fraser fir, seedlings and saplings must live to seed bearing age (Nicholas et al. 1992a). Pauly (1989) found germinal fir very scarce on Mt. Collins and predicted that it was not likely to see them in high numbers unless existing seedlings and saplings reached reproductive age. Seed bearing ages of fir usually occur at 20 to 30 years, with large seed crops occurring at 2–4 year intervals (USFS 1974). Since Eagar (1985) found open grown fir trees resistant to the adelgid in the Great Smoky Mountains until age 25, this may mean that open grown firs will be able to reach reproductive maturity before adelgid caused mortality occurs. However, Eagar (1984)

also found that firs become susceptible when they reach 5 cm dbh. Smith and Nicholas (2000) reported that Fraser fir in the Great Smoky Mountains did not produce cones until they reached 15-17 cm dbh. Smith (1997) also predicted that the dense "pole stands", as described by Cain (1935), would undergo intense intraspecific competition during the stand thinning stage at which the same time they become susceptible to stem infestation of the adelgid.

The fir that lives to maturity must be able to produce viable seed for continued survival of the species (Nicholas et al. 1992a). Nicholas et al. (1992a) observed a large seed crop year in 1987 with estimates of almost 2.5 million seeds per hectare at the highest elevations. However, 88 to 100% of the seeds were empty (n=549). Of the small percentage of seeds that were filled, 79% had germination capacity (Nicholas et al. 1992a). Fedde (1973a) observed seed production in Fraser fir infested by the woolly adelgid on Roan Mountain. He found that 82% of the trees sampled produced cones. The seeds that were produced in the infested trees were smaller in size, lighter, less viable, and more vulnerable to attack by the balsam fir chalcid (*Megastigmus specularis* Walley) (Fedde 1973b). Also infestation reduced the number of filled seeds by 40% (Fedde 1973b). Feede (1973a) concluded that the damage to the cone producing capacity of the tree is one of degree rather than kind.

The high densities of gap-invading thornless blackberry has made it difficult for fir seedlings to become established. Pauley (1989), and Pauley and Clebsch (1990) noted that blackberry interferes with the establishment of fir seedlings, although not with annual

growth rates. Hence seedling establishment are limited to dead wood substrates and shaded slopes (Pauley and Clebsch 1990).

Wide ranges of predictions were made about the future of the spruce-fir ecosystem. Eagar (1984) predicted a 35-60 year cycle of initial adelgid infestation, limited recovery and regeneration, reinfestation, etc. Rheinhardt (1984) predicted that the spruce-fir forests of the southern Appalachians may eventually resemble Whitetop, in southwestern Virginia, where fir became extirpated in the Xerothermic period (8500-3500 YBP). Witter and Ragenovich (1986) believed that Fraser fir may develop a resistance to the adelgid through selective pressure. Busing and Clebsch (1987) used a canopy gap model to simulate an adelgid outbreak in an old-growth spruce-fir stand. They predicted from this that a spruce dominated forest with low stand density would ultimately result. Based on observations of healthy regeneration and viable cones Witter (1988) held the optimistic opinion that Fraser fir will be a part of the Southern Appalachians for centuries to come. He also suggested that the balsam woolly adelgid will remain a part of this ecosystem. Busing and Clebsch (1988) found abundant recruitment of Fraser fir on Clingmans Dome. They suggested that the survival of fir depends on the adelgid infestation occurring at a time interval less than the time it takes for the trees to reach reproductive maturity (Busing and Clebsch 1988; Pauley and Clebsch 1990; Nicholas et al. 1992a). Nicholas et al (1992a) suggest that the understory densities of spruce and fir are dependant mainly on seed production, seed viability, germination, and survivorship of seedlings and germinals. Smith and Nicholas (2000) predicted that the southern

Appalachian fir populations in the future will be characterized by decreasing numbers of even-aged patches in different stages of regeneration and mortality.

## 3. OBJECTIVES

Recognizing the turbulent changing dynamics of the southern Appalachian spruce-fir forest, from ice age, to global warming, to fire, to logging, to the balsam woolly adelgid, this project aims to gain a better understanding of this seemingly unpredictable ecosystem. The objectives of this study are to evaluate overstory and understory structural dynamics on five mountain peaks in the GSMNP from 1990-2001. This project will quantify species composition, basal areas ($m^2$/ha), densities (stems/ha), ages, mortality rates, recruitment rates, diameter growth rates, and live verse dead stems. The stand type, elevation, aspect, slope, overstory composition, and disturbance history will be used as parameters to analyze the overstory and understory stand structure.

# 4. MATERIALS AND METHODS

## 4.1. Study Site

The Great Smoky Mountains National Park (GSMNP) holds 74% of the 26,608 ha of the spruce-fir in the southeast (Dull et al. 1988). Five peaks, encompassing nearly the entire Fraser fir range in the GSMNP, were selected for study areas: from northeast to southwest, Mount Sterling (1,781 m elevation), Mount Guyot (2,019 m), Mount LeConte (2,010 m), Mount Collins (1,887 m), and Clingmans Dome (2,025 m) (Figure 1). Major adelgid caused fir mortality occurred on Mount Sterling from 1970-1972, Mount Guyot 1980-1982, Mount LeConte 1982-1984, Mount Collins 1985-1987, and Clingmans Dome 1990-1992 (Smith 1997). The study area on each peak was within 100 m elevation of the mountain summit. According to Pyle (1984, 1985) none of the areas had likely been previously logged or burned.

## 4.2. Research Design

In 1990, a replicated series of stratified permanent plots were established after a systematic ground survey of the summit area was completed. Eight 400 $m^2$ (20 x 20 m) plots were established on each mountain, with two replicate plots in each of four stand types, for a total of forty 400 $m^2$ plots (Table 1). These plots were corrected for slope. The four stand types were Pure Live Fir (PLF; ≥65% of overstory (by basal area) in fir and ≥65% of fir living), Pure Dead Fir (PDF; ≥65% of overstory in fir, and ≥65% of fir dead), Mixed Live Fir (MLF; ≤35% of overstory in fir, and ≥65% of fir living), and Mixed Dead Fir (MDF; ≤35% of overstory in fir, and ≥65% of fir dead). The non-fir trees

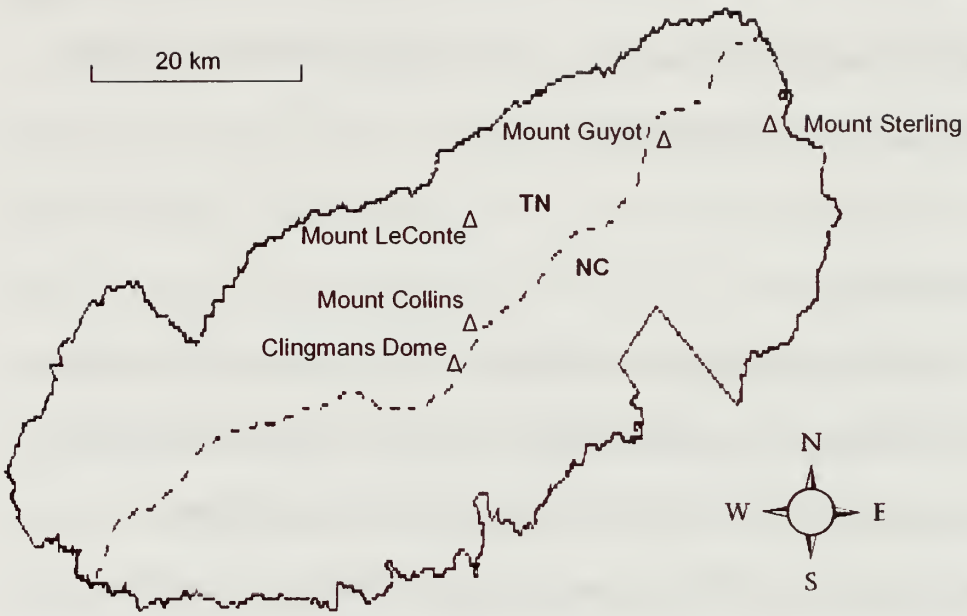


Figure 1. Great Smoky Mountains National Park spruce-fir study sites.

Table 1. Stand type criteria for original 1990 study design.

| **Pure Live Fir** | **Pure Dead Fir** |
|---|---|
| ≥65% of overstory (by basal area) in fir, and ≥65% of fir living | ≥65% of overstory in fir, and ≥65% of fir dead |
| **Mixed Live Fir** | **Mixed Dead Fir** |
| ≤35% of overstory in fir, and ≥65% of fir living | ≤35% of overstory in fir, and ≥65% of fir dead |

in a stand type were an unspecified mix of spruce and hardwoods. In four instances replicate plots meeting the stand type criteria were not met; one Mixed Live Fir (MLF) plot on Mount Guyot, one PLF and one PDF plot on Mount Sterling, and one PLF plot on Clingmans Dome. Therefore only 36 plots were used in 1990-91. In 2000 one PLF plot was added to Clingmans Dome, for a total of 37 plots.

### 4.3. Data Measurement

The plots were established and sampled in 1990 and 1991 by the Uplands Research Laboratory, GSMNP. They were re-sampled in 2000 and 2001. Sampling methodology followed the National Acidic Precipitation Assessment Program's Forest Response Program protocols (Zedaker et. al. 1988) and was the same as Nicholas et al. (1992a, 1992b) in earlier spruce-fir monitoring in the GSMNP.

Each overstory tree (≥5 cm diameter at breast height (DBH; 1.37 m high)) was mapped, measured for diameter, and given a three letter species code. Important comments included presence of cones, or adelgid presence or symptomology. Species considered shrubs, such as rhododendron (*Rhododendron* spp.) and smooth sumac (*Rhus glabra* L.), were not included in overstory. Canopy position, dominant, co-dominant, intermediate, or suppressed was estimated for each tree. Each overstory spruce and fir stem was classified into crown condition classes (class 1: 90-100% intact, class 2: 50-86% intact, class 3: 1-49% intact, class 4: recently dead, and class 5: old dead). Five of the biggest diameter live firs in the plot were cored and measured for height using a clinometer and a range pole. Cone data was collected, but was omitted from the study

because quality assurance control suggested that the data was inaccurate. Twenty-five 1x1 cm samples were taken to tally the number of adelgids on the bark of the Firs (Appendix A).

Sixteen randomly selected 2x2 m subplots, nested in each plot, were sampled for saplings and woody shrubs (≥1.37 m tall and <5 cm dbh). There were four subplots in each of four strips located in the north, west, south, and east quadrants. The species, basal diameter (15 cm above the ground), height, crown condition, and disturbance symptomology were determined for each of the plants. The term "shrub" refers to woody perennial species with a low, spreading growth form and multiple roots from a common root mass. The species considered shrubs were witch-hobble, rhododendron, sumac, elderberry, dog-hobble, ribes, and minnie-bush (Menziesia pilosa (Michx.) Jussieu). Suffrutescent sub-shrubs, such as *Rubus, Diervilla*, and *Hydrangea* were not included in this category. Sampling highbush blueberry and bearberry was determined to be too time consuming because it occurred frequently, and had a large number of stems. It was omitted from the study in 2000. However both species of *Vaccinum* were sampled in 1990-91.

One 1x1 m subplot was placed in each of the 16 2x2 m plots. In each of these subplots ground cover types (bare soil, twig/leaf litter, bare rock, bole, bryophytes/lichen, aerial woody debris, ground woody debris, stream/seep, and herb/sub-shrub) were estimated by the percent of the cover type that was visible when looking down on the subplot. Tree and shrub seedling occurrence by species and size/age classes (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) were

tallied. Fir were classified as under 4 years of age if they had no lateral branches, or bud scars from annual growth.

Ten destructive samples were taken from outside of each plot to determine the ages and conditions of fir seedling and saplings. Two trees from each of five size/age classes (1-4 years, 4 years-.25 m tall, .25 m-1 m, 1 m-1.37 m, and ≥1.37 m and <5 cm dbh) were cut at ground level. A cross section of the basal area of the stem was taken back to the lab for age analysis. The height of each tree was measured as well as the basal diameter (15 cm high). The basal diameters were measured twice, once on the minimum and once on the maximum axis. This reduces the error caused by stem variability. The tree was given a crown condition and a comment code. Root samples were taken from the two largest destructive samples to be tested for the presence of mycorrhizae.

Two 1x1 meter subplots in each quadrant were randomly selected to determine the vegetation in the herbaceous layer. The cover of each species was estimated by percent. Only the area of the plants that could be seen when looking down on the plot were included. For example if a blackberry grew over a common wood sorrel (*Oxalis montana* L.), only the blackberry would be included. Certain plants were not flowering depending on the time of year. Therefore it was difficult to determine the plants to the species level. In some cases only the genus was determined. Since certain shrubs such as *Vaccinium spp.* were not included in 2000 shrubs and saplings survey, they were included in the herbaceous survey.

Foliar samples were collected in order to determine the change in nutrient content over time. Approximately two one-gallon size bags of foliage in each plot were clipped with an even mix of current and last year's growth. The current year's foliage was separated from the previous years in the laboratory. Samples were dried in an oven and ground into a fine powder using a Wiley Mill. The samples were tested for carbon, nitrogen, potassium, calcium, magnesium, copper, iron, manganese, aluminum, lead, nickel, boron, and sulfur at North Carolina State University.

Each plot was measured for elevation, aspect, and slope. A linear scale was used by transforming the aspect according to the Beers et. al. (1966) method:

$A' = \cos(45 - A) + 1$

Where:

A=aspect in degress

A'=transformed aspect

This creates a linear scale that measures the distance from 45° and 225°. An aspect of 45° has a transformed aspect of 2 and an aspect of 225° has a transformed aspect of 0. For example the aspects of 310° and 140° have the same transformed aspect of .913 because they are both equidistant from 225°.

### 4.4. Data analysis.

All statistical analysis was done with SAS (SAS Institute 1999).

The paired Wilcoxon Signed Rank test, was used to assess the changes in the overstory, sapling, and seedling classes of 36 plots from 1990-91 to 2000-01. This nonparametric test was appropriate because the variables were not normally distributed. The variables used were densities (stems/ha) and basal areas ($m^2$/ha) of all major species groups (fir, spruce, mountain-ash, yellow birch, other hardwoods, and shrubs). Mean ages (yr) were assessed for Fraser fir only. A significance level of .10 was used.

Multiple regression was used to describe overstory and understory live fir, spruce, yellow birch, mountain-ash, and other hardwood basal area and density. A Monte Carlo bootstrapping method, with 1000 permutations, was used to test the significance of the models. Independent variables were elevation, aspect, slope, and the number of years since peak adelgid caused fir mortality. Before using regression, the aspect in degrees was transformed to a linear scale from 0 to 2 (Beers et al. 1966). The number of years since peak adelgid mortality was determined by mountain peak; Mt. Sterling 1971, Mt. Guyot 1981, Mt. LeConte 1983, Mt. Collins 1986, and Clingmans Dome 1991 (Smith 1997).

Mortality, recruitment (ingrowth), and growth rates of all major species groups between 1990-91 to 2000 were calculated. Recruited trees were less than 5.0 cm DBH at the initial sampling period but reached at least 5.0 cm DBH by 2000. In order to make comparisons with Nicholas (1992) the plots used were those over 1,800 m. One plot on

Clingmans Dome was left out because it was not sampled in 1990-91. The total number of plots used for the recruitment, growth, and mortality comparisons was 31.

# 5. RESULTS AND DISCUSSION

## 5.1. Live and Dead Overstory

### 5.1.1. Overall

There were no significant changes (90% confidence level, Wilcoxon signed rank test) in live overstory fir basal area ($m^2$/ha) from 1990-2000 (Table 2). However there was a significant increase in density from 697 stems/ha to 853 stems/ha (Table 2). Annual mortality rates of live overstory fir during this period were lower than rates found in the late 1980s (Nicholas 1992) (Table 3). The mean dbh growth rate of fir from 1990-91 to 2000 was .26 cm/year (Table 4). There were no significant changes in dead fir basal area and density.

The reason for the increase in live density and a reduced mortality rate of Fraser fir can be explained by the "pre adelgid" uneven-aged structure of the forest. The older cohort of fir suffered high amounts of mortality during the initial infestation (DeSelm and Bonner 1984; Busing and Clebsch 1988; Dull et al. 1988; Nicholas 1992). According to Eagar (1985) bark fissures on these larger trees allowed the adelgid easier access to the pheloderm, and thus made the trees more susceptible to the insect. Since the initial infestation, a sparse collection of advanced regeneration entered the overstory. This was reflected by a decrease in overstory mean dbh from 12 cm in the late 1940s (Osting and Billings, 1951) to 10 cm in 1990-91 (Table 5). These young trees were more resistant to adelgid attack because of their tight smooth bark which inhibited penetration (Eagar 1984). Hence this relict cohort of fir has seen less change in basal area over the last

Table 2. Basal area ($m^2$/ha ± SD) and density (stems/ha ± SD) of live overstory (≥5 cm dbh) species in the late 1940s (Oosting and Billings 1951), 1990-91, and 2000.

| Species | | *late 1940s | Year | | % change 1990-91 to 2000 | Wilcoxon Signed Rank Test p-value |
|---|---|---|---|---|---|---|
| | | | 1990-91 | 2000 | | |
| **Fir** | basal area ($m^2$/ha) | 16.85 | 10.21 ± 14.31 | 9.51 ± 9.38 | -7% | 0.4586 |
| | density (stems/ha) | 925 | 697 ± 1010 | 853 ± 577 | 22% | 0.0750 |
| **Spruce** | basal area ($m^2$/ha) | 25.98 | 18.74 ± 19.91 | 15.41 ± 15.68 | -18% | 0.1033 |
| | density (stems/ha) | 230 | 262 ± 300 | 256 ± 267 | -2% | 0.6936 |
| **Mountain-ash** | basal area ($m^2$/ha) | - | .78 ± 1.39 | .97 ± 1.68 | 24% | 0.0128 |
| | density (stems/ha) | - | 66 ± 122 | 63 ± 110 | -5% | 0.4531 |
| **Yellow birch** | basal area ($m^2$/ha) | - | 2.21 ± 5.85 | 2.12 ± 5.25 | -4% | 0.3757 |
| | density (stems/ha) | - | 61 ± 177 | 55 ± 159 | -10% | 0.3945 |
| **Other hardwood species** | basal area ($m^2$/ha) | - | 1.81 ± 3.91 | 1.70 ± 3.70 | -6% | 0.5905 |
| | density (stems/ha) | - | 109 ± 206 | 88 ± 156 | -19% | 0.5003 |
| **All species combined** | basal area ($m^2$/ha) | - | 33.75 ± 19.21 | 29.70 ± 15.87 | -12% | 0.0996 |
| | density (stems/ha) | - | 1195 ± 1122 | 1314 ± 598 | 10% | 0.1532 |

*From Oosting and Billings (1951), Great Smoky Mountains

Table 3. Mortality rates (%/year) of overstory (≥5 cm dbh) species between 1985-1989 and 1990-91-2000.

| | Fir | Spruce | Mountain-ash | Yellow Birch | Other Hardwood Species |
|---|---|---|---|---|---|
| **1985-1990*** | 7<br>n=538 | 2.2<br>n=229 | 11.7<br>n=-62 | 1.9<br>n=74 | - |
| **1990-91- 2000** | 3.1<br>n=1118 | 1.6<br>n=407 | 0.79<br>n=99 | 1.7<br>n=48 | 5.6<br>n=161 |

* From Nicholas (1992), Great Smoky Mountains 1830 – 1980 m elevation data.
n is # of live trees at beginning of survey period.

Table 4. Mean diameter growth rates (cm/year) of overstory (≥5 cm dbh) species between 1990-91-2000.

| | Fir | Spruce | Mountain-ash | Yellow Birch | Other Hardwood Species |
|---|---|---|---|---|---|
| **1990-91-2000** | 0.26<br>n=850 | 0.3<br>n=367 | 0.27<br>n=92 | 0.28<br>n=83 | 0.27<br>n=125 |

Table 5. Mean dbh (cm ± SD) of live overstory (≥5 cm dbh) species in the late 1940s (Oosting and Billings, 1951), 1990-91, and 2000.

| Species | *Mean dbh 1940s (cm) | Mean dbh 1990-91 (cm) | Mean dbh 2000 (cm) | % Change 1990-91 - 2000 | Wilcoxon Signed Rank Test p-value |
|---|---|---|---|---|---|
| **Fir** | 12.04 | 10.17 ± 5.46 | 10.78 ± 3.77 | 6% | 0.0640 |
| **Spruce** | 30.33 | 24.07 ± 13.39 | 22.29 ± 12.43 | -7% | 0.7826 |
| **Mountain-ash** | - | 3.33 ± 5.35 | 5.31 ± 6.97 | 198% | 0.2961 |
| **Yellow Birch** | - | 6.79 ± 11.63 | 7.12 ± 12.20 | 5% | 0.1677 |
| **Other Hardwood Species** | - | 6.33 ± 7.41 | 6.78 ± 8.30 | 7% | 0.1756 |

*From Oosting and Billings (1951), Great Smoky Mountains

decade than during the peak adelgid attack. Smith and Nicholas (1999) suggested that the initial wave of adelgid destruction was over by the early 1990s.

The overstory fir left after the first wave of the balsam woolly adelgid was sparse. Live fir basal area and density in the pre-adelgid late 1940s were 119% and 33% more respectively than in 1990-91 (Oosting and Billings 1951) (Table 2).

From the late 1940s to 1990-91 red spruce basal area decreased by 7.24 $m^2$/ha (Table 2). There are several possible explanations for this decrease. The first is that this shallow rooted species (Crandall 1958) likely suffered from "thinning shock" because of the death of nearby fir (Nicholas et al. 1992a). This effect is created primarily from the increased exposure to wind, light and temperature fluctuations or a predisposing climatic and atmospheric deposition interaction (Johnson 1991; Shepard et al. 1995). For example, large amounts of acidic deposition, common in the Southern Appalachians (Johnson and Lindberg 1992), have been shown to reduce calcium and magnesium availability (Johnson 1991). These nutrients are important in regulating red spruce health. Red spruce density, however, increased by 32 stems/ha from the late 1940s to 1990.

There were no significant changes in live overstory red spruce basal area or density from 1990-91 to 2000 (Table 2). However there were significant increases in dead spruce basal area and density. This indicates that recently dead overstory spruce were replaced by recruited trees from 1990-91 to 2000. The increase in standing dead spruce illustrates the decreasing effects of wind exposure that was suffered following the death of high numbers of overstory fir. Since 1990-91 the overstory fir component increased, lessening the effects of wind on standing dead spruce.

There was a reduction in red spruce annual mortality rates since the late 1980s (Nicholas 1992) (Table 3). This suggests that the negative effects of the "thinning shock" on live spruce are declining. Many of the larger more exposed spruces died prior to this study, and left behind were smaller trees, less exposed to the elements. This was illustrated by the reduction in mean diameters of live overstory spruce from 30.33 cm the late 1940s to 24.07 cm in 1990-91 (Table 5) (Oosting and Billings 1951). The mean dbh growth rate of spruce from 1990-91 to 2000 was .30 cm/year (Table 4).

There were no significant changes in live and dead mountain-ash basal and density since 1990-91 (Table 2). Likewise, the recruitment rate was low (.53 %/year) (Table 6). The annual mortality rates were reduced from 11.7 % in the late 1980s to .79% from 1990-91 to 2000 (Table 3) (Nicholas 1992). The initial high mortality rate for this species was hypothesized to be linked to the mountain-ash sawfly, another invasive European insect (Nicholas 1992). This reduction in mortality suggests that damage caused by the sawfly has peaked. Perhaps this indicates a positive response to increased levels of light and/or a decline in sawfly populations in the region. Current mountain-ash health studies in the Great Smoky Mountains National Park have not indicated the presence of sawflies for over 10 years (Johnson 2003, personal communication). The mean dbh growth rate of mountain-ash from 1990-91 to 2000 was .27 cm/year (Table 4).

No significant changes were found with live or dead overstory yellow birch basal or density (Table 2). This is consistent with Nicholas (1992) who predicted that the yellow birch population in GSMNP would exhibit little change from 1989 to 2009. However, it is possible that the sample size was not sufficient due to the low densities of this species.

Mortality rates were reduced from 1.9 to 1.7 stems/ha/year from the late 1980s to the current study (Table 3) (Nicholas 1992). The recruitment rate exceeds mortality only slightly (Table 3, Table 6). The yellow birch mean dbh growth rate was .28 cm/year (Table 4).

There were seven species in the other hardwood class in 1990-91; serviceberry, red maple, mountain maple, American beech, pin cherry, black cherry, and red oak. In 2000 all of these species were present with the addition of one sugar maple. The most common species in both of these time periods was mountain maple, black cherry, and American beech. There were no significant changes in live and dead basal area and density of this species class from 1990-91 to 2000 (Table 2). This is not surprising due to the low densities of these trees. A larger sample size would be needed to detect any significant changes in this species class.

**5.1.2. By Stand Type**

The greatest amounts of live fir basal area were found in the two live fir stand types (PLF: 20.7 $m^2$/ha, and MLF: 8.0 $m^2$/ha) (Figure 2). Live fir density was highest in the PLF and PDF stand types (1,325 and 906 stems/ha) (Figure 3). Despite the highest levels of live fir basal area, the live fir stand types underwent the greatest reductions in live fir basal area and density since 1990-91 (Figure 2, Figure 3). These reductions were the result of adelgid caused mortality in the overstory. In 1990-91 the PLF and the MLF had the highest levels of live fir basal area and density and consequently suffered the largest loss. The high level of live fir density in the PDF stand type indicates recruitment of fir

Table 6. Recruitment rates (%/year) of overstory (≥5 cm dbh) species between 1990-91-2000.

| | Fir | Spruce | Mountain-ash | Yellow Birch | Other Hardwood Species |
|---|---|---|---|---|---|
| **1990-91- 2000** | 4.55<br>n=1118 | 1.8<br>n=407 | 0.53<br>n=99 | 1<br>n=48 | 7.9<br>n=161 |

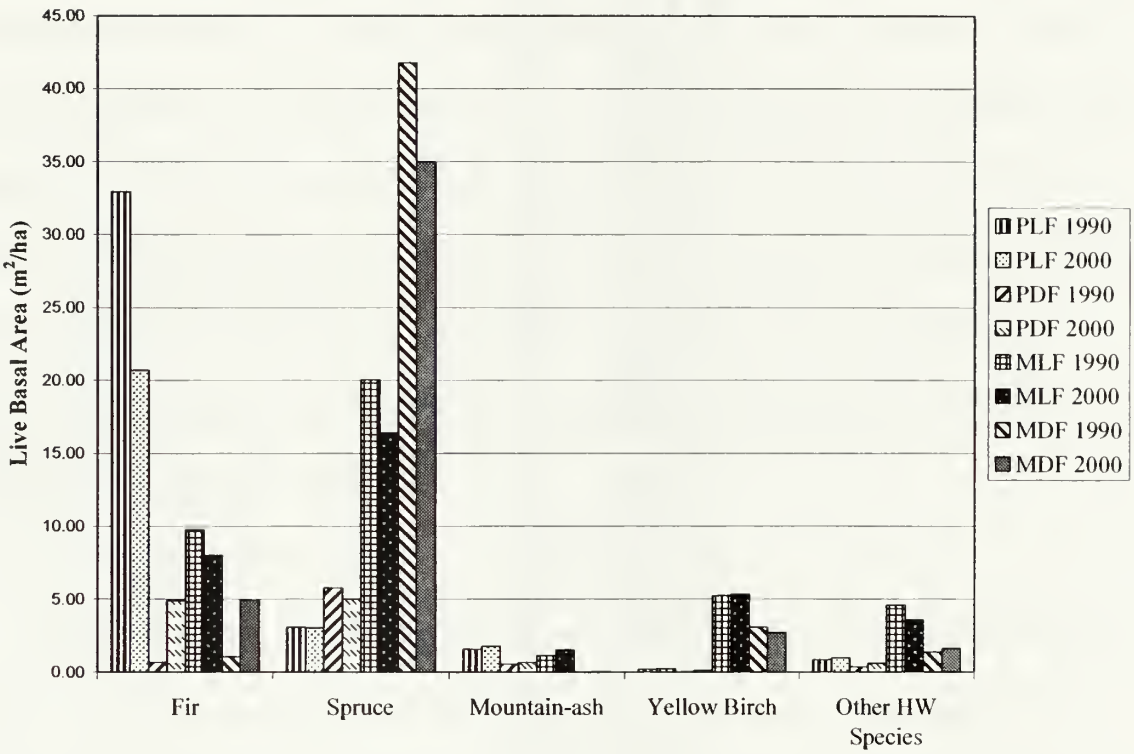


Figure 2. Mean basal areas ($m^2$/ha) of live overstory (≥5 cm dbh) species by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir) in 1990-91 and 2000.

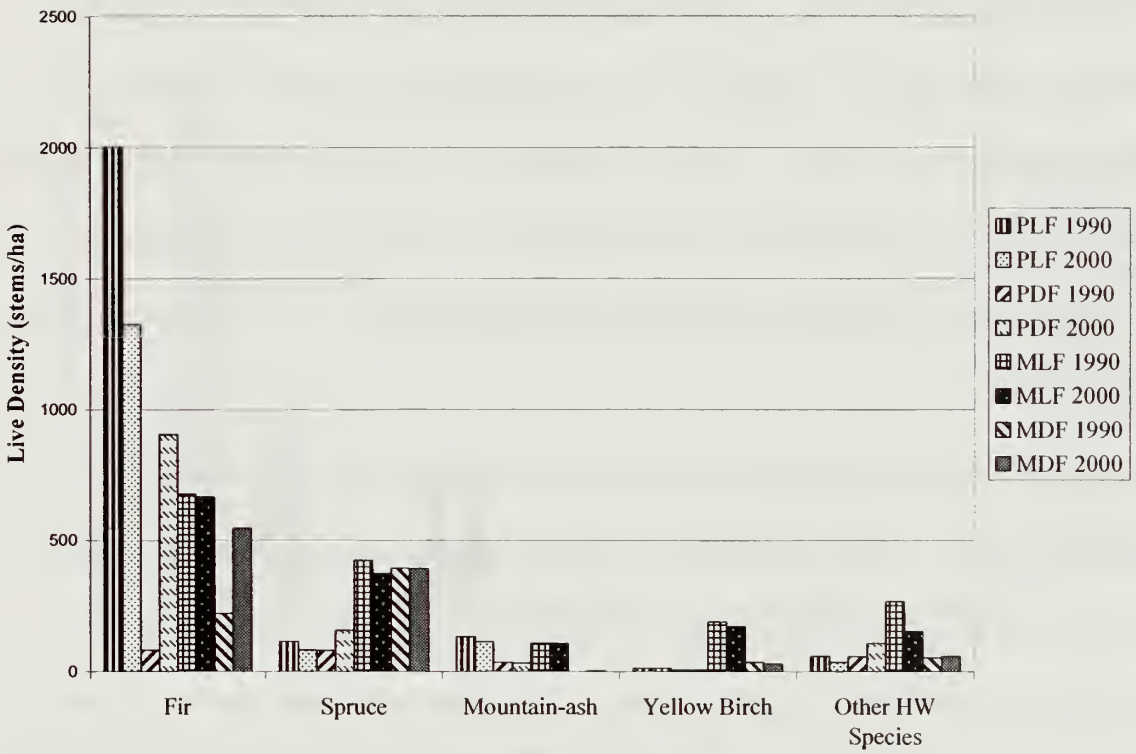


Figure 3. Mean densities (stems/ha) of live overstory (≥5 cm dbh) species by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir) in 1990-91 and 2000.

stems into the overstory since 1990-91. This type had the lowest density of live fir in 1990-91 and thus had ample space for new recruits.

The only stand types to increase in dead fir basal area from 1990-91 were the PLF and MLF stand types (16.7 and 4.1 $m^2$/ha respectively) (Figure 4). Furthermore, these were the only stand types to increase in dead fir density (627 and 192 stems/ha respectively) (Figure 5). This is consistent with the high losses of live fir basal area and density in these stand types that were mentioned above. Dead fir basal area and density were highest in the PLF and PDF stand types (Figure 4, Figure 5). The dead standing fir in the PLF stand type were killed by the adelgid from 1990-91. The dead standing fir in the PDF were killed prior to this study, as indicated by the high basal areas and densities in 1990-91 (Figure 4, Figure 5). This illustrates Fraser fir's ability to remain part of the overstory for over 10 years following mortality.

Live spruce basal area was highest in the mixed stand types (MDF: 35.0 $m^2$/ha, MLF: 16.4 $m^2$/ha) (Figure 2). These stand types also had the greatest live spruce densities (MDF: 393 stems/ha, MLF: 375 stems/ha) (Figure 3). In 1990-91 they were also highest in live spruce basal area and density (Figure 2, Figure 3). All of the stand types decreased in live spruce basal area (Figure 2). The largest decrease was shown in the mixed stand types (Figure 2). The PDF was the only stand type to increase in live spruce density (81 to 158 stems/ha) (Figure 3). Dead spruce basal area and density was highest in the mixed stand types.

The number of overstory species, excluding spruce and fir, was greater in the mixed dead fir stands (9) than the two pure fir stands (6). This is because the criteria for the mixed stand

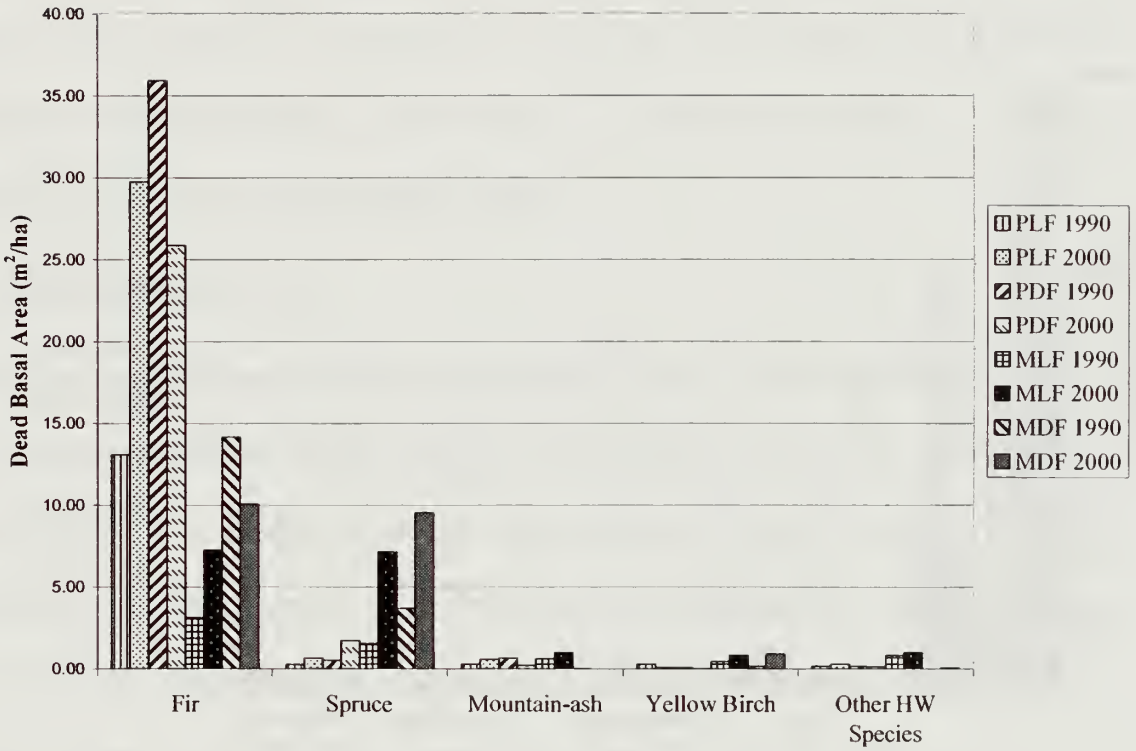


Figure 4. Mean basal areas ($m^2$/ha) of dead overstory (≥5 cm dbh) species by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir) in 1990-91 and 2000.

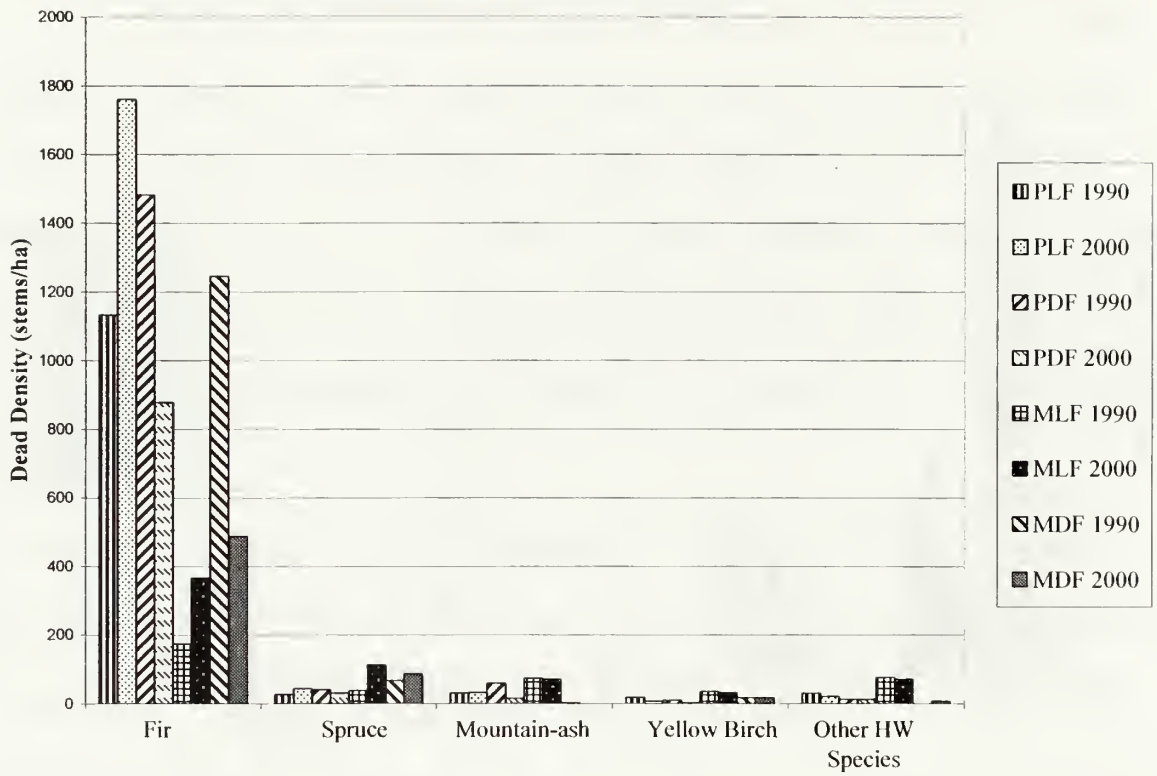


Figure 5. Mean densities (stems/ha) of dead overstory (≥5 cm dbh) species by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir) in 1990-91 and 2000.

types was that ≤35% of the basal area was made up of overstory fir. Naturally this would allow space for other species. The highest basal area of live mountain-ash (1.8 $m^2$/ha) was found in the PLF type (Figure 2). Live yellow birch basal area was highest in the MLF type (5.4 $m^2$/ha) (Figure 2). The other hardwood species class also had the highest live basal area (3.6 $m^2$/ha) in the MLF type (Figure 2). The highest density of live mountain-ash (114 stems/ha) was found in the PLF type (Figure 3). Live yellow birch density (172 stems/ha) was highest in MLF type (Figure 3). The density of the other hardwood species class (153 stems/ha) was greatest in the MLF type (Figure 3).

### 5.1.3. By Mountain Peak

The five mountain peaks showed a great deal of variability. Since past studies have shown that fir increases in abundance with elevation (Whittaker 1956), it is not surprising that live fir basal area and density was greatest on Mt. Guyot (16.4 $m^2$/ha, and 1,143 stems/ha respectively) (Figure 6, Figure 7). Likewise, basal area and density of live fir was lowest on Mt. Sterling, the peak with the lowest elevation (6.2 $m^2$/ha and 496 stems/ha respectively) (Figure 6, Figure 7). Mount Collins showed the largest change in live fir basal area from 1990-91 to 2000 (10.9 to 3.8 $m^2$/ha respectively) (Figure 6). Despite this decrease, Mt. Collins exhibited the greatest increase in density (309 to 869 stems/ha). Mt. LeConte was the only mountain that decreased in fir basal area and density (Figure 6, Figure 7). This was also noted by Jenkins (2003) when he observed significant decreases in both basal area and density of overstory fir on Mt. LeConte from 1979 to 2001.The largest amount of dead fir

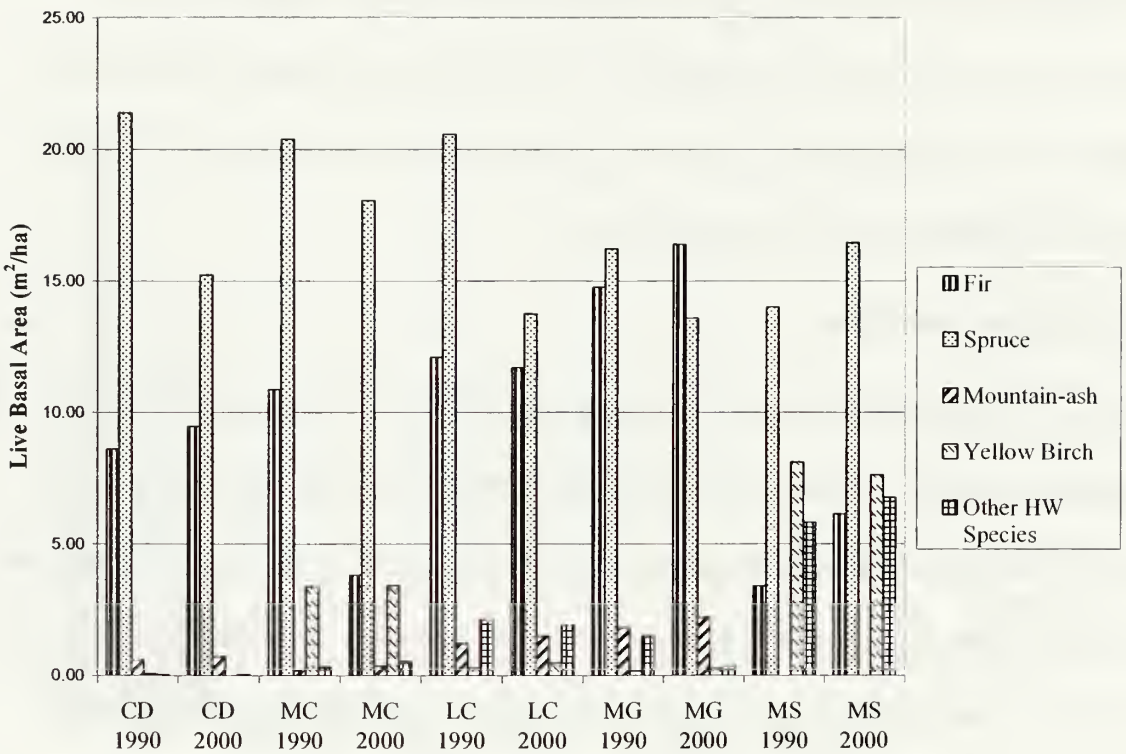


Figure 6. Mean basal areas ($m^2$/ha) of live overstory (≥5 cm dbh) species by mountain peak (CD-Clingmans Dome, MC-Mount Collins, LC-Mount LeConte, MG-Mount Guyot, MS-Mount Sterling) in 1990-91 and 2000.

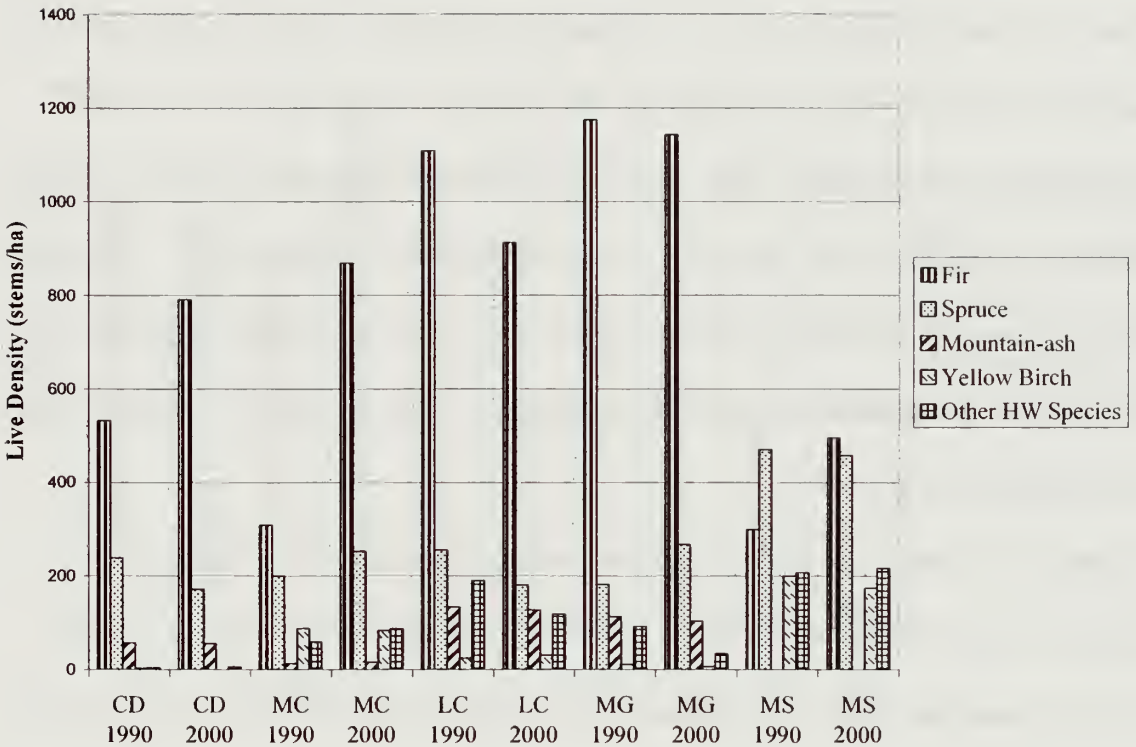


Figure 7. Mean densities (stems/ha) of live overstory (≥5 cm dbh) species by mountain peak (CD-Clingmans Dome, MC-Mount Collins, LC-Mount LeConte, MG-Mount Guyot, MS-Mount Sterling) in 1990-91 and 2000.

basal area was on Mt. Collins (24.57 $m^2$/ha) (Figure 8). Mt. Guyot held the greatest amount of dead fir density (1361 stems/ha) (Figure 9).

With the exception of Mt. Guyot, spruce basal area exceeded fir on all the mountain peaks (Figure 6). In 1990-91 all of the mountains had greater spruce basal area than fir. Fir density exceeded spruce density on all the mountain peaks in 2000 (Figure 7). The highest densities of live spruce were found on Mt. Sterling (458 stems/ha) (Figure 7). This was also the case in 1990-91 (471 stems/ha) (Figure 7). Mt. Guyot and Mt. Collins were the only peaks to increase in spruce density from 1990-91 to 2000, and Mt Sterling was the only peak to increase in spruce basal area. Mean dbh of live mature spruce ranged from 13.6 cm on Mt. Guyot to 30.7 cm on Clingman's Dome. Live spruce density and basal area was greater than dead spruce density and basal area on all mountain peaks (Figure 6, Figure 7, Figure 8, Figure 9). This was the same in 1990-91.

The greatest number of overstory species excluding spruce and fir was found on Mt. Sterling (11), while Clingmans Dome had only 2. Oostings and Billings (1951) mentioned yellow birch, mountain maple, and mountain-ash as being present in almost every spruce-fir type stand. In 2000 there was no mountain maple found on Mt. Sterling, and Mt. LeConte, and no mountain-ash on Mt. Sterling. The highest basal area of live mountain-ash was found on Mt. Guyot in 1990-91 and 2000 (1.8 and 2.2 $m^2$/ha respectively) (Figure 6). Mountain-ash density was highest on Mt. LeConte for both sampling periods (134 and 128 stems/ha respectively) (Figure 7). Yellow birch and mountain maple had a greater density and basal

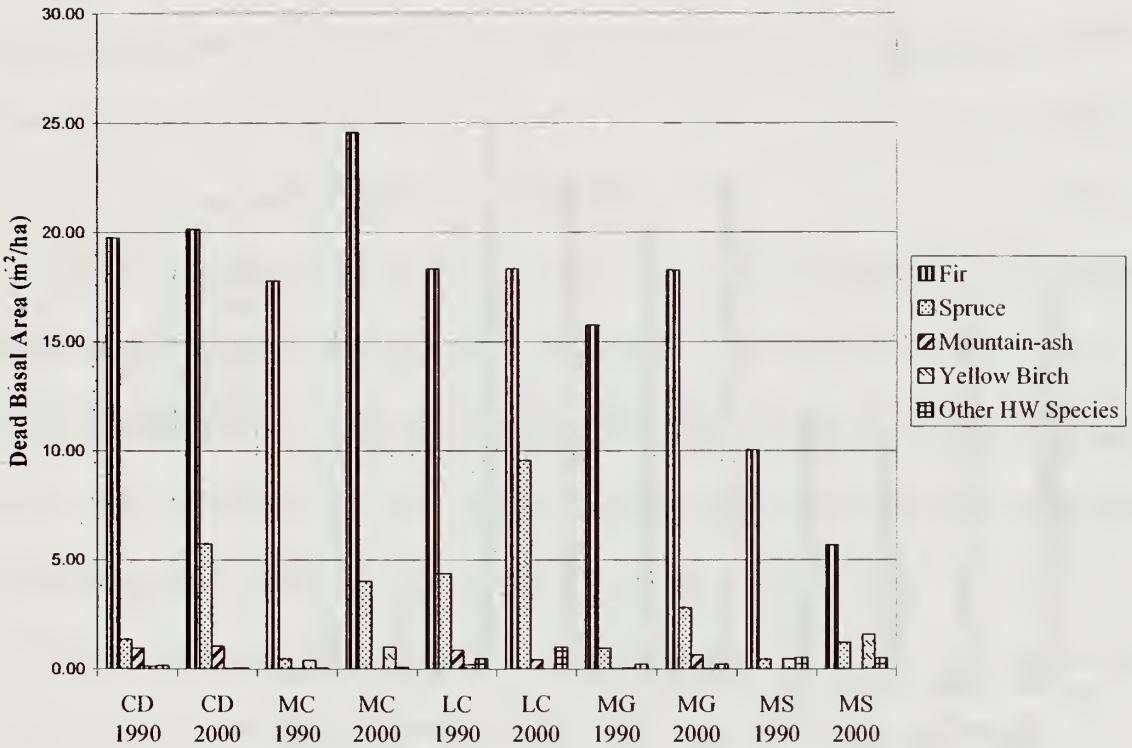


Figure 8. Mean basal areas ($m^2$/ha) of dead overstory (≥5 cm dbh) species by mountain peak (CD-Clingmans Dome, MC-Mount Collins, LC-Mount LeConte, MG-Mount Guyot, MS-Mount Sterling) in 1990-91 and 2000.

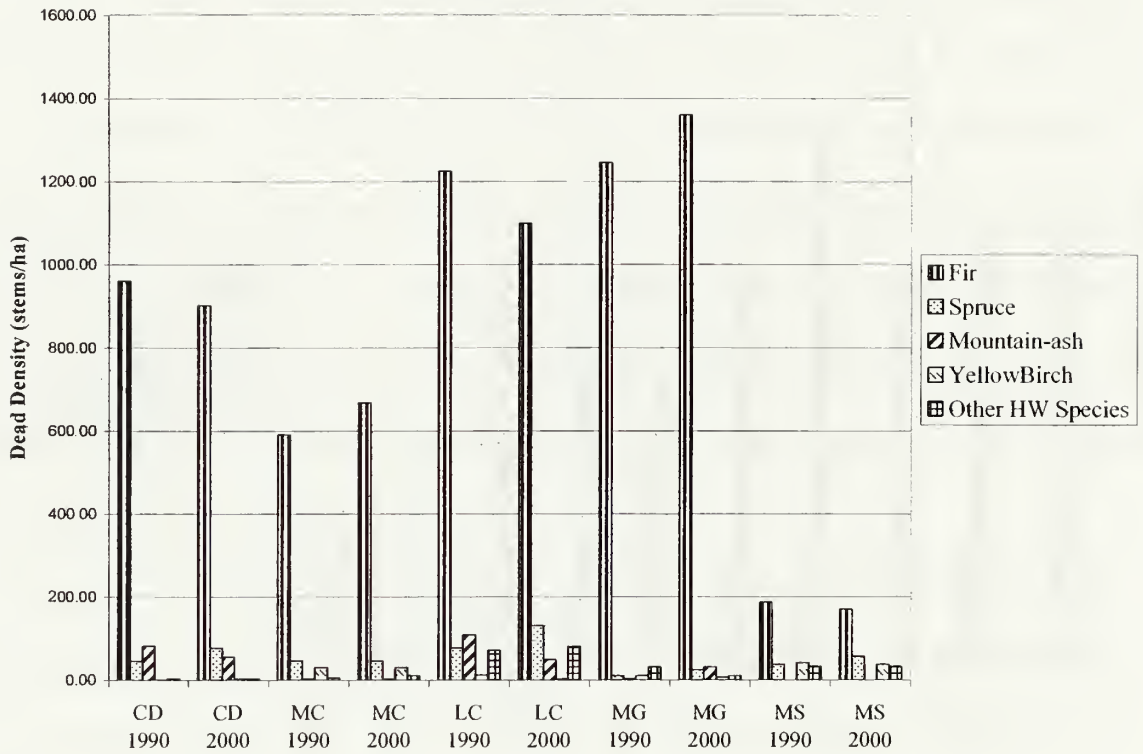


Figure 9. Mean densities (stems/ha) of dead overstory (≥5 cm dbh) species by mountain peak (CD-Clingmans Dome, MC-Mount Collins, LC-Mount LeConte, MG-Mount Guyot, MS-Mount Sterling) in 1990-91 and 2000.

area on the lower peaks of Mt. Sterling and Mt. Collins. The same trend was noted in 1990-91 with these species. LeConte held the highest density and basal area of fire cherry, another less common species in the spruce fir forests according to Oosting and Billings (1951). This was also found in 1990-91. Because of the low elevation, Mt. Sterling supported the greatest diversity of hardwood species. The lowest basal area and density of live hardwoods was found on Clingmans Dome. Smith (1997) attributed this partially to high amounts of exposure to wind and ice storms.

### 5.1.4. Comparisons With Site Characteristics

Multiple regression was performed on live fir, spruce, mountain-ash, yellow birch, and other hardwood basal area ($m^2$/ha) and density (stems/ha) with the 2000-01 data. A Monte Carlo bootstrapping method, with 1000 permutations, was used to test the significance of the models. Independent variables used were elevation, the number of years since peak adelgid caused fir mortality (YSM), slope, and linearly transformed aspect (Beers et al. 1966).

Fir basal area significantly correlated with elevation and YSM (Table 7). This correlation with elevation is consistent with past studies which have shown that fir increases in dominance with elevation (Cain 1935; Whittaker 1956). The positive correlation with YSM was also found by Bonner (1979) who observed greater fir densities and basal areas with time since peak adelgid caused fir mortality. In 1990-91, however, no such trends with fir basal area were found (Smith 1997).

In 1990-91 elevation and YSM were significant predictors of fir density (Smith 1997). Each regression coefficient was positive indicating that fir density increased with elevation and YSM. The positive correlation with elevation was consistent with past

Table 7. Non-parametric regression of basal area ($m^2$/ha) and density (stems/ha) of live overstory (≥5 cm dbh) fir, spruce, mountain-ash, yellow birch, and other hardwood species on elevation, years since major adelgid caused fir mortality (YSM), percent slope, and linearly transformed aspect [1] in 2000.

| | $R^2$ | Elevation | YSM | Slope | Aspect[1] | $P^2$ |
|---|---|---|---|---|---|---|
| **Fir basal area ($m^2$/ha)** | .2792 | 0.0793 | 0.7157 | - | - | 0.004 |
| **Spruce density (stems/ha)** | 0.2138 | -1.3239 | - | 5.3885 | - | 0.020 |
| **Spruce basal area ($m^2$/ha)** | 0.1625 | - | - | 0.4111 | - | 0.010 |
| **Mountain-ash density (stems/ha)** | 0.2049 | 0.5581 | - | -1.9178 | - | 0.024 |
| **Mountain-ash basal area ($m^2$/ha)** | 0.2370 | 0.0086 | - | -0.0376 | - | 0.010 |
| **Yellow birch density (stems/ha)** | 0.2271 | -0.8848 | - | - | - | 0.001 |
| **Yellow birch basal area ($m^2$/ha)** | 0.3305 | -0.0354 | - | - | - | 0.010 |
| **Hardwood density (stems/ha)** | 0.2259 | -0.6942 | - | - | 88.8495 | 0.019 |
| **Hardwood basal area ($m^2$/ha)** | 0.3177 | - | 0.3260 | - | - | 0.002 |

[1] The transformed aspect is a linear scale from 0-2 that measures the distance from 225° (southwest) (Beers et al. 1966).

[2] Degrees of freedom for significance tests in 1990-91 is 35 and 36 in 2000.

studies (Cain 1935; Korstian 1937; Oosting and Billings 1951; Whittaker 1956). However, no significant correlations were found with fir density in 2000.

Spruce density was significantly negatively correlated with elevation, and positively correlated with slope (Table 7). The same trend was found in 1990-91 (Smith 1997). Consistently Busing et al. (1993) and Smith (1997) found that spruce dominated more on the steeper slopes where there was less exposure to wind. Other studies have shown negative correlations with elevation (Oosting and Billings 1951; Whittaker 1956; Busing et al. 1993). Spruce basal area was correlated with slope and not elevation in both sampling periods (Smith 1997).

Mountain-ash density and basal area were significantly positively correlated with elevation for 1990-91 and 2000 (Table 7) (Smith 1997). Another study showed a similar trend with elevation (Ramseur 1960). Mountain-ash basal area negatively correlated with slope and mountains-ash density positively correlated with slope. However the effects of slope on mountain-ash populations have not been documented in previous work, and these inconsistencies can not be explained.

Yellow birch density correlated negatively with elevation (Table 7). This is also consistent with a past study (Ramseur 1960).

The other hardwood species class density correlated negatively with elevation and positively with aspect in 2000. The correlation with elevation is consistent with past studies (Korstian 1937; Crandall 1958). Since most of the high elevation hardwood species are shade intolerant, and northeastern aspects receive the least sunlight, it is surprising that there is a positive correlation with aspect. However, no other studies have shown that aspect has any influence on

hardwood density. Hardwood basal area correlated only with YSM indicating that hardwood species were able to take advantage of the extra available light from the canopy gaps caused by the adelgid.

### 5.1.5. Changes in Stand Types

In 1990-91 there were eight PLF, nine PDF, nine MLF, and ten MDF plots (Table 8). Of the eight PLF plots only one remained PLF in 2000, three became PDF, and the other four did not meet any of the stand type criteria. Six of the PDF plots remained the same while the other 3 failed to meet any of the criteria. Three of the MLF remained the same, one became MDF, and the other 5 did not fall into any of the categories. Of the 10 MDF plots seven remained the same, one became MLF, and the other two did not meet any criteria.

Since half of the 36 plots changed stand types, and of these half 14 did not fit any of the four types, the stand type designation was determined to be obsolete. These criteria are arbitrary numbers with little scientific merit.

Table 8. Stand type designations (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir) of plots in 1990-91 and 2000.

| Plot | Stand Type 1990-91 | Stand Type 2000 |
|---|---|---|
| **CD-1** | PLF | none |
| **LC-1** | PLF | PLF |
| **LC-2** | PLF | none |
| **MC-1** | PLF | PDF |
| **MC-2** | PLF | PDF |
| **MG-1** | PLF | none |
| **MG-2** | PLF | none |
| **MS-1** | PLF | none |
| **CD-2** | PLF | PDF |
| **CD-3** | PDF | PDF |
| **CD-4** | PDF | none |

Table 8. Cont.

| Plot | Stand Type 1990-91 | Stand Type 2000 |
|---|---|---|
| **LC-3** | PDF | PDF |
| **LC-4** | PDF | PDF |
| **MC-3** | PDF | PDF |
| **MC-4** | PDF | none |
| **MG-3** | PDF | PDF |
| **MG-4** | PDF | PDF |
| **MS-3** | PDF | none |
| **CD-5** | MLF | none |
| **CD-6** | MLF | none |
| **LC-5** | MLF | none |
| **LC-6** | MLF | none |
| **MC-5** | MLF | MDF |
| **MC-6** | MLF | none |
| **MG-5** | MLF | MLF |
| **MS-5** | MLF | MLF |
| **MS-6** | MLF | MLF |
| **CD-7** | MDF | MDF |
| **CD-8** | MDF | MLF |
| **LC-7** | MDF | MDF |
| **LC-8** | MDF | MDF |
| **MC-7** | MDF | MDF |
| **MC-8** | MDF | MDF |
| **MG-7** | MDF | none |
| **MG-8** | MDF | none |
| **MS-7** | MDF | MDF |
| **MS-8** | MDF | MDF |

## 5.2. Live and Dead Understory

### 5.2.1. Overall

Fraser fir saplings (≥1.37 m tall, <5 cm dbh) significantly increased by 1,713 stems/ha since 1990-91 (Table 9). Additionally the fir seedlings in size class S4 (1.01 m-1.36 m tall) increased by 571 stems/ha (Table 10). This increase in density was a result of the S1 (1-4 years), S2 (4-.25 m tall), and S3 (.26 m-1.0 m tall) size class responding positively to the surplus of space in the overstory caused by the balsam woolly adelgid. Similarly, DeSelm and Boner (1984) found large increases in fir understory after 10 years of adelgid caused overstory mortality. The smallest three fir seedling classes decreased in density from 1990-91 to 2000. One explanation is the competition for space from the S4 class and the sapling layer (Table 10). Another possibility is the desiccation of the moss and peat layer from increased levels of sunlight. Beck (1990) suggests that soil desiccation is the most limiting factor in fir seedling establishment.

Spruce saplings also significantly increased by 270 stems/ha (Table 9). There was also an increase in density in the S4 size class. Since 1990-91 the spruce in the S1 and S2 size classes were recruited into the S4 and sapling size classes (Table 9, Table 10).

The spruce in the smallest two seedling size classes decreased in density since 1990-91. This indicates a void of several years in reproduction of red spruce. Korstian (1937) presented three limiting factors in the natural reproduction of red spruce: 1) seed supply 2) competing vegetation 3) and soil and moisture. Hart (1965) estimated good spruce seed crops to occur every 3 to 8 years. This interval in seed crops is a possible reason for the decrease in the smallest two seedling classes. The second possibility is that the decreases in the S1 and S2 classes were caused by competition for space from the S4 and sapling layer. The third limiting factor, low soil

Table 9. Mean densities (stems/ha ± SD) of live sapling (≥1.37 m tall, <5 cm dbh) species in 1990-91 and 2000.

| Species | 1990-91 (stems/ha) | 2000 (stems/ha) | % Change 1990-91 to 2000 | Wilcoxon Signed Rank Test p-value |
|---|---|---|---|---|
| **Fir** | 981 ± 1,000 | 2,694 ± 2,463 | 175% | 0.0951 |
| **Spruce** | 135 ± 280 | 405 ± 510 | 200% | <0.0001 |
| **Mountain-ash** | 35 ± 100 | 165 ± 526 | 371% | 0.0454 |
| **Yellow birch** | 26 ± 70 | 55 ± 166 | 112% | 0.5391 |
| **Other hardwood species** | 117 ± 347 | 46 ± 208 | -61% | 0.6936 |
| **Shrubs** | 1,389 ± 2,275 | 1,145 ± 1,716 | -18% | 0.6941 |
| **All species combined** | 2,682 ± 2223 | 4,510 ± 4,929 | 68% | 0.2740 |

Table 10. Mean densities (stems/ha ± SD) of live seedling size class (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) species in 1990-91 and 2000.

| Species | Seedling Size Class | 1990-91 (stems/ha) | 2000 (stems/ha) | % Change 1990-91 to 2000 | Wilcoxon Signed Rank Test p-value |
|---|---|---|---|---|---|
| **Fir** | S1 | 10,503 ± 25,669 | 1,419 ± 3,345 | -86% | 0.0005 |
| | S2 | 14,444 ± 26,515 | 2,855 ± 6,273 | -80% | <0.0001 |
| | S3 | 8,524 ± 20,058 | 3,622 ± 4,486 | -58% | 0.0580 |
| | S4 | 747 ± 1384 | 1,318 ± 1,942 | 76% | 0.0130 |
| | total | 34,218 ± 54,300 | 9,213 ± 10,787 | -73% | <0.0001 |
| **Spruce** | S1 | 4,410 ± 8,072 | 590 ± 1,176 | -87% | 0.0006 |
| | S2 | 8,507 ± 17,117 | 1,406 ± 3,023 | -83% | 0.0026 |
| | S3 | 1,163 ± 1,960 | 1,285 ± 2,175 | 10% | 0.5600 |
| | S4 | 87 ± 265 | 503 ± 1,136 | 5% | 0.0195 |
| | total | 14,167 ± 25,933 | 3,682 ± 5,931 | -74% | 0.0012 |
| **Mountain-ash** | S1 | 955 ± 1802 | 3,649 ± 17,185 | 282% | 0.2139 |
| | S2 | 503 ± 919 | 101 ± 346 | -80% | 0.0020 |
| | S3 | 330 ± 676 | 0 | -100% | 0.0020 |
| | S4 | 35 ± 208 | 51 ± 227 | 46% | 1.0000 |
| | total | 1,823 ± 2,760 | 3,801 ± 17,370 | 109% | 0.0059 |
| **Yellow birch** | S1 | 1,285 ± 3,774 | 0 | 100% | <0.0001 |
| | S2 | 69 ± 199 | 0 | 100% | 0.1250 |
| | S3 | 17 ± 104 | 0 | 100% | 1.0000 |
| | S4 | 0 | 0 | 0% | - |
| | total | 1,372 ± 3,870 | 0 | -100% | <0.0001 |

Table 10 Cont.

| Species | Seedling Size Class | 1990-91 (stems/ha) | 2000 (stems/ha) | % Change 1990-91 to 2000 | Wilcoxon Signed Rank Test p-value |
|---|---|---|---|---|---|
| **Other hardwood species** | S1 | 521 ± 1,535 | 118 ± 719 | -77% | 0.1172 |
| | S2 | 139 ± 636 | 17 ± 103 | -88% | 0.2500 |
| | S3 | 87 ± 371 | 17 ± 103 | -80% | 0.2104 |
| | S4 | 17 ± 104 | 17 ± 103 | 0% | 1.0000 |
| | total | 764 ± 1,651 | 169 ± 829 | -78% | 0.0225 |
| **Shrubs** | S1 | 486 ± 734 | 608 ± 2,112 | 25% | 0.4231 |
| | S2 | 139 ± 636 | 220 ± 662 | 58% | 0.9119 |
| | S3 | 4,219 ± 6,742 | 929 ± 2,087 | -78% | <0.0001 |
| | S4 | 938 ± 1,827 | 389 ± 876 | -59% | 0.0338 |
| | total | 5,885 ± 8,715 | 2,145 ± 5,241 | -64% | <0.0001 |
| **All species combined** | S1 | 18160 ± 27,135 | 6,368 ± 18,884 | -65% | 0.0005 |
| | S2 | 23,906 ± 34,888 | 4,561 ± 8,629 | -81% | <0.0001 |
| | S3 | 14,340 ± 21,619 | 5,818 ± 6,249 | -59% | 0.0006 |
| | S4 | 1,823 ± 2,248 | 2,264 ± 2,981 | 24% | 0.3765 |
| | total | 60,816 ± 63,794 | 22,980 ± 42,041 | -62% | <0.0001 |

moisture caused by the increased sun exposure after adelgid caused overstory deterioration, could also explain this void in seedlings. No significant changes were found in the S3 size class.

Mountain-ash sapling density increased from 35 to 165 stems/ha (Table 9). This shade intolerant species likely thrived in response to the increased sunlight made available from the overstory deterioration. The vigorous sapling cohort could soon replace the mature mountain-ash trees that suffered high levels of mortality in the late 1980s, possibly due to the invasive insect, the mountain-ash sawfly (*Pristiphora geniculata* Hartig.) (Nicholas et al. 1992b).

Little change was found in the yellow birch saplings and seedlings from 1990-91 to 2000 (Table 9, Table 10). This is consistent with Nicholas (1992) who predicted that the yellow birch population in the Smoky Mountains would undergo little change from 1989 to 2009. Since this is an intermediate shade tolerant species (Erdmann 1990) no increased levels of abundance would be expected in response to the increased levels of light.

There were four understory species in the other hardwood class in 1990-91 and 2000; mountain maple, pin cherry, red maple, and American beech. From 1990-91 to 2000 there were no changes in density of the sapling or seedling classes. Due to the sparse nature of the other hardwood species in this ecosystem it is difficult to detect change with such a small sample size.

There were seven understory shrub species in 1990-91; minie bush (*Menziesia pilosa* (Michx.) Juss), catawba rosebay (*Rhododendron catawbiense* Mich.), piedmont

rhododendron (*Rhododendron minus* Mich.), Appalachian gooseberry (*Ribes rotundifolium* Mich.), elderberry, and witch-hobble. In 2000 there were only three species; catawba rosebay, smooth sumac (*Rhus glabra* L.), and witch hobble. Although it appears that the diversity of species decreased considerably over a ten year period, the three species absent in 2000 were very low in number in 1990-91 (minie bush, n=1; piedmont rhododendron, n=6; Appalachian gooseberry, n=2). In both of these sampling periods witch hobble was the most common shrub. The only shrub understory class that exhibited significant change was S3 which showed a reduction from 4,219 to 929 stems/ha (Table 9, Table 10). Shrub densities however are confounded by the fact that *Vaccinium* spp. was not sampled in 2000, and thus left out of the analysis. Without *Vaccinium* spp., an abundant shrub in this ecosystem (Crandall 1958; Crandall 1958; Ramseur 1960; Ramseur 1960), it would be frivolous to make statements about the shrub seedlings and saplings.

The fir sapling cohort not only increased in density since 1990-91 but also in vigor. The mean ages of saplings were 13 years younger in 2001 than in 1990-91 indicating an accelerated growth rate in response to the past overstory deterioration (Table 11). Smith and Nicholas (2000) observed a similar phenomenon when noting that the dominant and co-dominant fir are younger in age on earlier infested mountains than recently infested mountains. They suggested that young fir are growing faster under greater canopy openness, and rapidly replacing the overstory. Reductions in ages were also noted in the seedling size classes S1 and S4, and in the overstory.

Table 11. Mean ages (yr ± SD) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)), sapling (≥1.37 m tall, and <5 cm dbh), and overstory (≥5 cm dbh) fir in 1990-91 and 2000.

| Stem Size | Age in 1990-91 | Age in 2001 | % Change 1990-91 to 2000 | Wilcoxon Signed Rank Test p-value |
|---|---|---|---|---|
| **S1** | 5 ±2 | 3 ± 2 | -40% | <0.0001 |
| **S2** | 9 ± 3 | 10 ± 5 | 11% | 0.2745 |
| **S3** | 21 ± 28 | 14 ± 5 | -33% | 0.2133 |
| **S4** | 25 ±7 | 17 ± 6 | -28% | 0.0003 |
| **sapling** | 32±12 | 19 ± 9 | -41% | <0.0001 |
| **overstory** | 58 ± 22 | 36 ± 12 | -38% | 0.0079 |

### 5.2.2. By Stand Type

The PDF stand type had the highest density of Fraser fir saplings (4,063 stems/ha) (Table 12, Figure 10). This stand type also had the lowest total overstory basal area and density in 1990-91 (Table 2). This provided ample space encouraging the growth of advanced regeneration. Since one of the criteria for the pure stands was to have ≥65 overstory basal area in fir, there was evidently a sufficient seed source (Table 1). The MLF stand type held the lowest density of fir saplings (Table 12, Figure 10). One explanation is that this type had low fir densities in the two largest seedling classes in 1990-91 (Figure 11). Hence there were low numbers of seedlings recruited into the sapling cohort from 1990-91 to 2000. Another reason is that the selection criteria for the mixed stand types was to have ≤35% overstory basal area in fir (Table 1). This limited the number of potential seed sources.

The PLF stand type held the highest densities of fir in the S1, S2, and S3 size class (Table 12, Figure 10). Although this stand type suffered the greatest losses in overstory fir basal area and density from 1990-91 to 2000 (Figure 2, Figure 3) there was evidently enough viable seed to produce sufficient regeneration. The PDF stand type had the highest density of fir in the S4 size class (Table 12, Figure 10). The high levels of fir density in the S1, S2, and S3 size class in 1990-91 exhibited growth and were recruited into the S4 and sapling class (Table 12, Figure 10, Figure 11,).

Table 12. Mean densities (stems/ha ± SD) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) Fraser fir in 1990-91 and 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | PLF | | PDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 38,594 ± 45,667 | 4,653 ± 5,661 | 1,875 ± 2,001 | 486 ± 977 |
| S2 | 32,969 ± 46,704 | 8,264 ± 10,665 | 10,694 ± 17,805 | 903 ± 1,852 |
| S3 | 10,000 ± 16,174 | 4,792 ± 5,087 | 17,847 ± 36,414 | 2,597 ± 2,729 |
| S4 | 1,250 ± 2,339 | 1,528 ± 2,883 | 694 ± 1,102 | 2,014 ± 2,183 |
| All Seedlings | 82,813 ± 81,334 | 19,236 ± 13,866 | 31,111 ± 54,939 | 6,000 ± 5,999 |
| Saplings | 1,133 ± 1,277 | 2,917 ± 5,419 | 1,180 ± 1,260 | 4,063 ± 5,975 |
| Total Understory | 83,945 ± 81,061 | 22,153 ± 15,188 | 32,292 ± 54,695 | 10,063 ± 10,675 |

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | MLF | | MDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 4,167 ± 5,422 | 417 ± 1,250 | 1,500 ± 2,149 | 250 ± 437 |
| S2 | 11,181 ± 18,303 | 1,806 ± 3,833 | 5,938 ± 6,911 | 688 ± 906 |
| S3 | 2,569 ± 2,604 | 4,653 ± 6,282 | 4,313 ± 5,694 | 2,563 ± 3,326 |
| S4 | 625 ± 1,250 | 764 ± 1,201 | 500 ± 645 | 1,000 ± 1,110 |
| All Seedlings | 18,542 ± 25,453 | 7,639 ± 10,476 | 12,250 ± 13,104 | 4,500 ± 5,203 |
| Saplings | 868 ± 894 | 1,128 ± 1,534 | 781 ± 616 | 2,672 ± 2,898 |
| Total Understory | 19,410 ± 25,930 | 87,67 ± 10,969 | 13,031 ± 13,150 | 7,172 ± 7,721 |

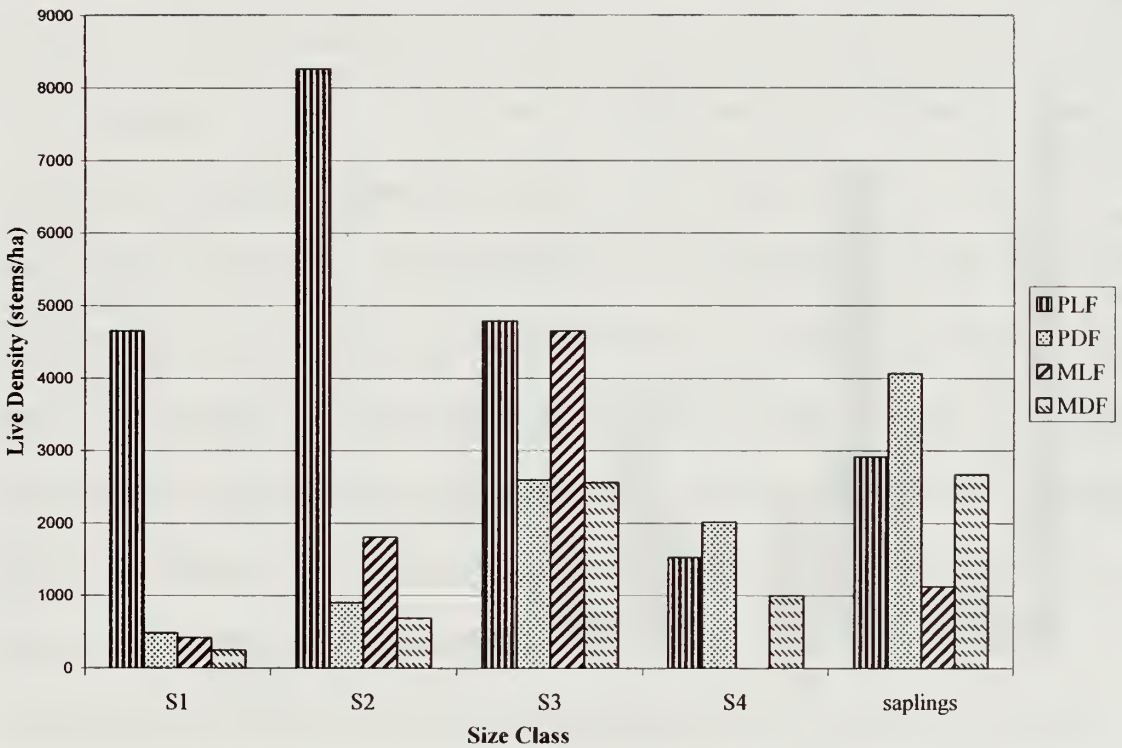


Figure 10. Mean densities (stems/ha) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, <5 cm dbh) Fraser fir in 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

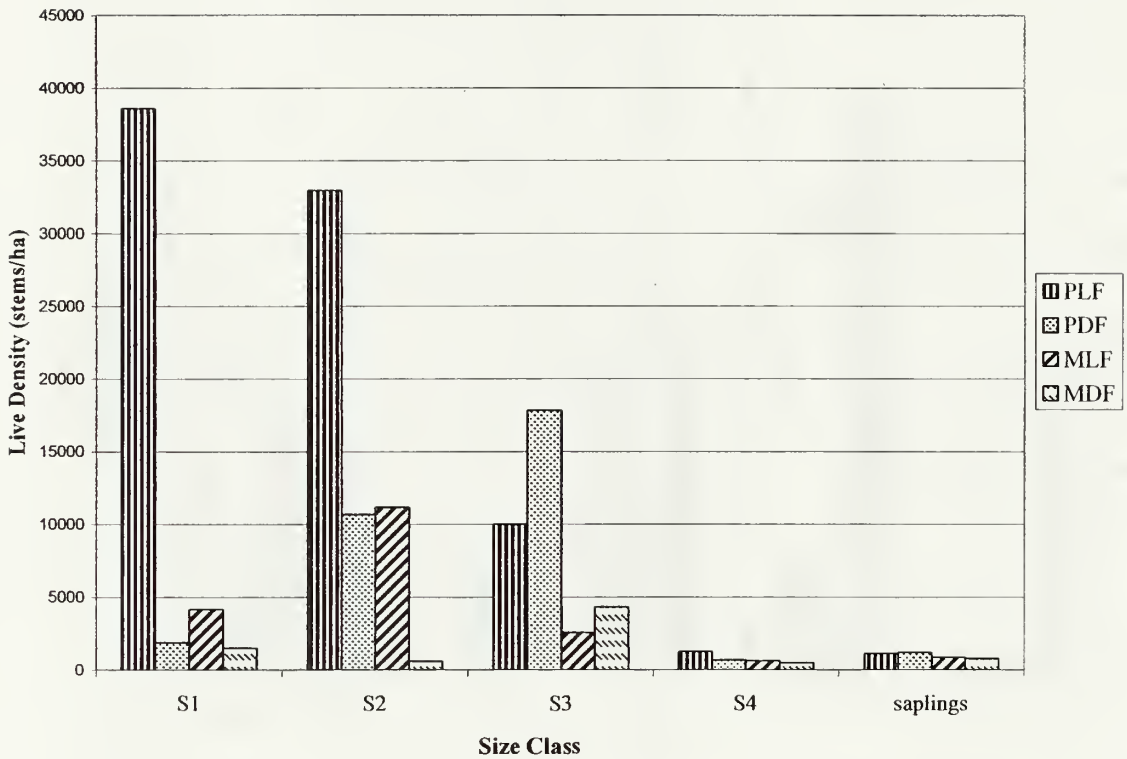


Figure 11. Mean densities (stems/ha) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) Fraser fir in 1990-91 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

Live spruce sapling densities were greatest in the MDF stand type (688 stems/ha) (Table 13). In 1990-91 this stand type held the highest densities of spruce seedlings (Table 13). From 1990-91 to 2000 these seedlings were recruited into the sapling cohort. The MDF type also has the highest densities of the S1 and the S3 spruce seedling size classes (938 and 1,875 stems/ha respectively), illustrating successful regeneration of spruce in this stand type (Table 13). The S2 live spruce seedling size class density was greatest in the PLF stand type (2,361 stems/ha), and the S4 size class was greatest in the PDF stand type (903 stems/ha) (Table 13).

Mountain-ash understory density was highest in the PLF stand type (11,458 stems/ha) (Table 14). Other studies have shown that this species is more prevalent in the pure fir stands (Ramseur 1960). The PLF stand type also exhibited the greatest increase in mountain-ash understory from 1990-91 to 2000 (9,878 stems/ha). The overstory in this stand type showed the greatest reductions in basal area and density from 1990-91 to 2000 (Figure 2, Figure 3). This provided increased levels of light favorable to the shade intolerant mountain-ash understory.

The PDF stand type had no yellow birch understory in 2000 (Table 15). This is not surprising because this type had the lowest basal area and density of overstory yellow birch in both sampling periods (Figure 2, Figure 3). Relative to the spruce and fir the yellow birch understory had extremely low densities overall. Therefore it is not practical to make generalizations about the stand types in respect to yellow birch.

Table 13. Mean densities (stems/ha ± SD) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) red spruce in 1990-91 and 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | PLF | | PDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1,250 ± 2,339 | 694 ± 1,102 | 1,111 ± 2,894 | 0 |
| S2 | 4,609 ± 8,517 | 2,361 ± 4,859 | 1,389 ± 2,826 | 208 ± 625 |
| S3 | 1,016 ± 2,163 | 1,181 ± 2,285 | 694 ± 960 | 625 ± 1,036 |
| S4 | 0 | 278 ± 634 | 139 ± 276 | 903 ± 1,852 |
| All Seedlings | 6,875 ± 12,642 | 4,514 ± 7,634 | 3,333 ± 5,616 | 1,736 ± 3,010 |
| Saplings | 20 ± 55 | 208 ± 406 | 139 ± 264 | 434 ± 657 |
| Total Understory | 6,895 ± 12,653 | 4,722 ± 7,685 | 3,472 ± 5,645 | 2,170 ± 3,327 |

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | MLF | | MDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 2,847 ± 5,098 | 625 ± 1,654 | 11,313 ± 11,977 | 938 ± 1,188 |
| S2 | 5,833 ± 14,987 | 1,458 ± 2,898 | 20,438 ± 25,430 | 1,438 ± 2,146 |
| S3 | 347 ± 329 | 1,250 ± 2,847 | 2,438 ± 2,771 | 1,875 ± 2,224 |
| S4 | 69 ± 208 | 69 ± 208 | 125 ± 395 | 688 ± 1,081 |
| All Seedlings | 9,097 ± 19,861 | 3,403 ± 6,359 | 34,313 ± 38,355 | 4,938 ± 6,211 |
| Saplings | 208 ± 462 | 260 ± 322 | 156 ± 181 | 688 ± 517 |
| Total Understory | 9,306 ± 19,768 | 3,663 ± 6,337 | 34,469 ± 38,367 | 5,625 ± 6,650 |

Table 14. Mean densities (stems/ha± SD ) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) mountain-ash in 1990-91 and 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | PLF | | PDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1,641 ± 1,766 | 3,750 ± 9,657 | 764 ± 1,201 | 0 |
| S2 | 703 ± 1,178 | 139 ± 417 | 625 ± 1,250 | 0 |
| S3 | 313 ± 668 | 0 | 347 ± 833 | 0 |
| S4 | 0 | 139 ± 417 | 139 ± 417 | 0 |
| All Seedlings | 2,656 ± 3,386 | 4,028 ± 9,632 | 1,875 ± 2,073 | 0 |
| Saplings | 0 | 139 ± 213 | 17 ± 52 | 35 ± 104 |
| Total Understory | 2,656 ± 3,386 | 4,167 ± 9,588 | 1,892 ± 2,068 | 35 ± 104 |

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | MLF | | MDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1,181 ± 2,732 | 11,250 ± 33,750 | 375 ± 1189 | 0 |
| S2 | 208 ± 442 | 139 ± 417 | 500 ± 710 | 125 ± 395 |
| S3 | 139 ± 276 | 0 | 500 ± 823 | 0 |
| S4 | 0 | 0 | 0 | 63 ± 198 |
| All Seedlings | 1,528 ± 3,279 | 11,389 ± 34,167 | 1,375 ± 2,531 | 188 ± 422 |
| Saplings | 52 ± 111 | 69 ± 158 | 63 ± 151 | 391 ± 975 |
| Total Understory | 1,580 ± 3,375 | 11,458 ± 34,141 | 14,38 ± 2,662 | 578 ± 1,219 |

Table 15. Mean densities (stems/ha ± SD) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) yellow birch in 1990-91 and 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | PLF | | PDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1,016 ± 1,635 | 0 | 69 ± 208 | 0 |
| S2 | 78 ± 221 | 0 | 0 | 0 |
| S3 | 78 ± 221 | 0 | 0 | 0 |
| S4 | 0 | 0 | 0 | 0 |
| All Seedlings | 1,172 ± 1,651 | 0 | 69 ± 208 | 0 |
| Saplings | 39 ± 72 | 17 ± 52 | 0 | 0 |
| Total Understory | 1,211 ± 1,697 | 17 ± 52 | 69 ± 208 | 0 |

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | MLF | | MDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1,250 ± 2,670 | 0 | 2,625 ± 6,587 | 0 |
| S2 | 0 | 0 | 188 ± 302 | 0 |
| S3 | 0 | 0 | 0 | 0 |
| S4 | 0 | 0 | 0 | 0 |
| All Seedlings | 1,250 ± 2,670 | 0 | 2,813 ± 6,759 | 0 |
| Saplings | 17 ± 52 | 35 ± 69 | 47 ± 106 | 156 ± 295 |
| Total Understory | 1,267 ± 2,661 | 35 ± 69 | 2,859 ± 6,855 | 156 ± 295 |

All of the stand types showed reductions in the other hardwood species class understory (Table 16). Similar to the yellow birch, this class had an extremely low understory density overall, making it difficult to see patterns among the stand types.

Understory shrub densities were highest in the PLF stand type (6,875 stems/ha) (Table 17). The PDF stand types showed the greatest reduction in shrubs (5,250 stems/ha) (Table 17).

The number of understory species in 1990-91 were higher than the number of species in 2000 in all of the stand types. The largest reduction was in the MDF type. In 1990-91 this type had 11 species and was reduced to 5 in 2000.

**5.2.3. By Mountain**

Mt. Collins and Mt. LeConte showed the greatest increase in fir saplings from 1990-91 to 2000 (3,886 and 3,555 stems/ha respectively) (Table 18). These peaks also had the greatest reduction in overall overstory basal area encouraging the growth of advanced regeneration during this time (Figure 6). Mt. Guyot and Mt. Sterling were the only peaks to decrease in fir sapling density from 1990-91 to 2000 (357 and 312 stems/ha respectively) (Table 18).

Mt. Sterling was the only peak to increase in fir seedlings (1,770 stems/ha) (Figure 12, Figure 13, Table 18). Nevertheless this peak had the lowest densities of fir seedlings and saplings in both sampling periods. This is probably because it is the peak with the lowest elevation. Studies have shown that elevation is positively correlated with Fraser fir (Whittaker 1956). All of the other peaks exhibited large decreases in fir seedling densities (Table 18).

Table 16. Mean densities (stems/ha ± SD) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) other hardwood species class in 1990-91 and 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | PLF | | PDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1,172 ± 2,597 | 0 | 486 ± 1,458 | 0 |
| S2 | 0 | 0 | 0 | 0 |
| S3 | 0 | 0 | 139 ± 417 | 69 ± 208 |
| S4 | 0 | 0 | 69 ± 208 | 0 |
| All Seedlings | 1,172 ± 2,597 | 0 | 694 ± 1,513 | 69 ± 208 |
| Saplings | 0 | 17 ± 52 | 365 ± 615 | 139 ± 417 |
| Total Understory | 1,172 ± 2,597 | 17 ± 52 | 1,059 ± 1,704 | 208 ± 625 |

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | MLF | | MDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 486 ± 1,241 | 486 ± 1,458 | 63 ± 198 | 0 |
| S2 | 417 ± 1,250 | 69 ± 208 | 1,254 ± 264 | 0 |
| S3 | 0 | 0 | 188 ± 593 | 0 |
| S4 | 0 | 69 ± 208 | 0 | 0 |
| All Seedlings | 903 ± 1,627 | 625 ± 1,654 | 375 ± 791 | 0 |
| Saplings | 35 ± 104 | 35 ± 69 | 63 ± 198 | 0 |
| Total Understory | 938 ± 1,609 | 660 ± 1,648 | 438 ± 979 | 0 |

Table 17. Mean densities (stems/ha ± SD) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)) and sapling (≥1.37 m tall, >5 cm dbh) shrubs in 1990-91 and 2000 by stand type (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | PLF | | PDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 391 ± 742 | 139 ± 417 | 208 ± 442 | 1,042 ± 2,119 |
| S2 | 78 ± 221 | 139 ± 276 | 139 ± 276 | 278 ± 833 |
| S3 | 1,875 ± 3,044 | 278 ± 551 | 5,278 ± 8,525 | 625 ± 1,250 |
| S4 | 391 ± 880 | 139 ± 417 | 1,111 ± 2,114 | 278 ± 551 |
| All Seedlings | 2,734 ± 3,966 | 694 ± 960 | 6,736 ± 10,638 | 2,222 ± 4,309 |
| Saplings | 742 ± 1,701 | 399 ± 1,028 | 1,319 ± 2,345 | 1,042 ± 1,262 |
| Total Understory | 3,477 ± 5,449 | 1,094 ± 1,839 | 8,056 ± 12,536 | 3,264 ± 5,195 |

| Size Class | Stand Type | | | |
|---|---|---|---|---|
| | MLF | | MDF | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 486 ± 521 | 1,319 ± 3,730 | 813 ± 1,023 | 0 |
| S2 | 417 ± 1,250 | 347 ± 1,042 | 313 ± 607 | 125 ± 264 |
| S3 | 5,833 ± 8,822 | 2,361 ± 3,708 | 3,688 ± 5,183 | 500 ± 874 |
| S4 | 972 ± 2,483 | 764 ± 1390 | 1,188 ± 1,599 | 375 ± 844 |
| All Seedlings | 7,708 ± 11,651 | 4,792 ± 9,448 | 6,000 ± 6,998 | 1,000 ± 1,619 |
| Saplings | 2,118 ± 2,733 | 2,084 ± 2,534 | 1,313 ± 2,332 | 1,063 ± 1,502 |
| Total Understory | 9,826 ± 13,496 | 6,875 ± 11,715 | 7,313 ± 9,196 | 2,063 ± 2,606 |

Table 18. Mean densities (stems/ha ± SD) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) Fraser fir in 1990-91 and 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

| Size Class | Mountain Peak | | | | | |
|---|---|---|---|---|---|---|
| | CD | | LC | | MC | |
| | 1990-91 | 2000 | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 5,893 ± 4,403 | 547 ± 1,313 | 8,203 ± 12,876 | 3,906 ± 4,504 | 5,078 ± 9,817 | 0 |
| S2 | 15,714 ± 19,617 | 2,031 ± 1,941 | 14,531 ± 17,840 | 3,359 ± 5,519 | 24,922 ± 48,260 | 1,094 ± 1,326 |
| S3 | 5,446 ± 7,845 | 4,297 ± 5,614 | 18,281 ± 38,814 | 5,109 ± 4,849 | 11,250 ± 15,368 | 4,609 ± 5,132 |
| S4 | 982 ± 1,294 | 1,875 ± 1,567 | 391 ± 742 | 1,406 ± 2,133 | 1,719 ± 2,309 | 2,188 ± 2,932 |
| All Seedlings | 28,036 ± 27,588 | 8,750 ± 6,984 | 41,406 ± 55,578 | 13,781 ± 9,777 | 42,969 ± 73,538 | 7,891 ± 8,647 |
| Saplings | 893 ± 923 | 1,934 ± 2,210 | 1,074 ± 997 | 4,629 ± 6,484 | 1,055 ± 1,290 | 4,941 ± 5,161 |
| Total Understory | 28,928 ± 28,286 | 10,684 ± 8,171 | 42,481 ± 55,293 | 18,410 ± 11,854 | 44,023 ± 73,721 | 12,832 ± 12,971 |

| Size Class | Mountain Peak | | | |
|---|---|---|---|---|
| | MG | | MS | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 31,607 ± 53,281 | 446 ± 1,181 | 1,563 ± 3,254 | 2,292 ± 5,613 |
| S2 | 11,964 ± 17,442 | 4,732 ± 11,714 | 1,771 ± 2,969 | 3,438 ± 7,518 |
| S3 | 3,304 ± 4,756 | 2,411 ± 3,335 | 1,563 ± 1,296 | 833 ± 645 |
| S4 | 357 ± 709 | 536 ± 983 | 104 ± 255 | 208 ± 323 |
| All Seedlings | 47,232 ± 72,283 | 8,125 ± 15,865 | 5,000 ± 6,386 | 6,771 ± 13,552 |
| Saplings | 1,183 ± 1,220 | 826 ± 962 | 625 ± 474 | 313 ± 313 |
| Total Understory | 48,415 ± 71,713 | 8,951 ± 15,529 | 5,625 ± 6,521 | 7,083 ± 13,496 |

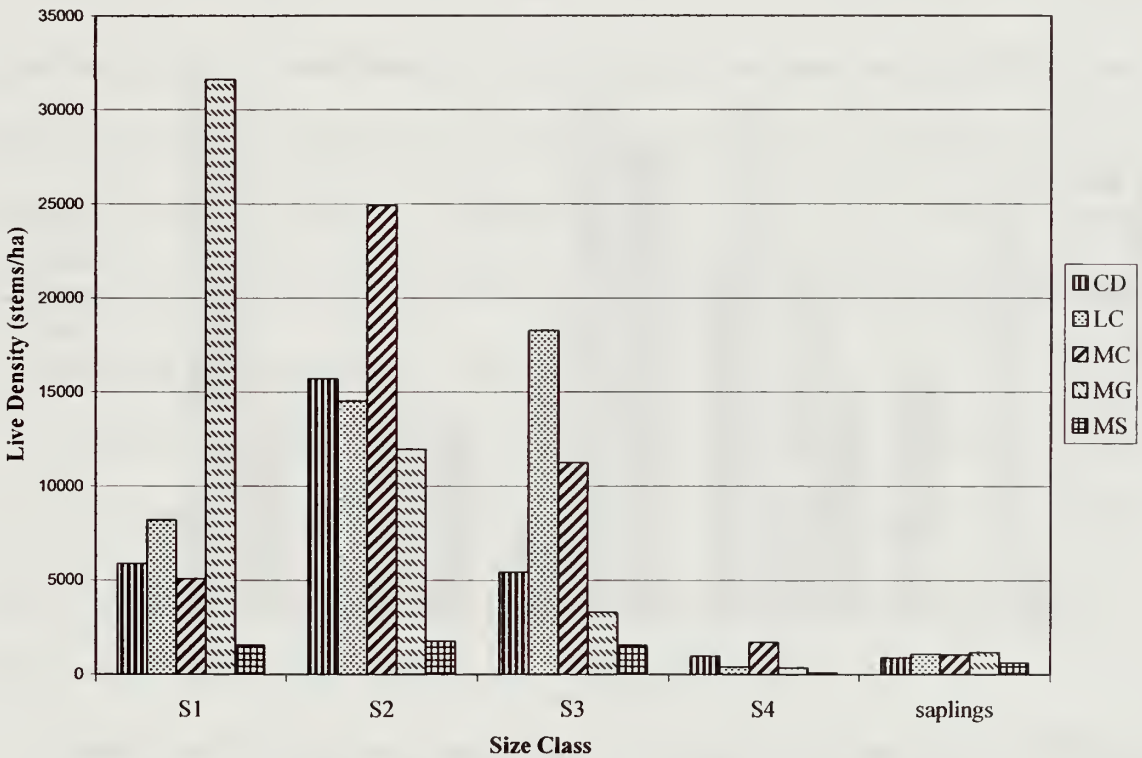


Figure 12. Mean densities (stems/ha) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) Fraser fir in 1990-91 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

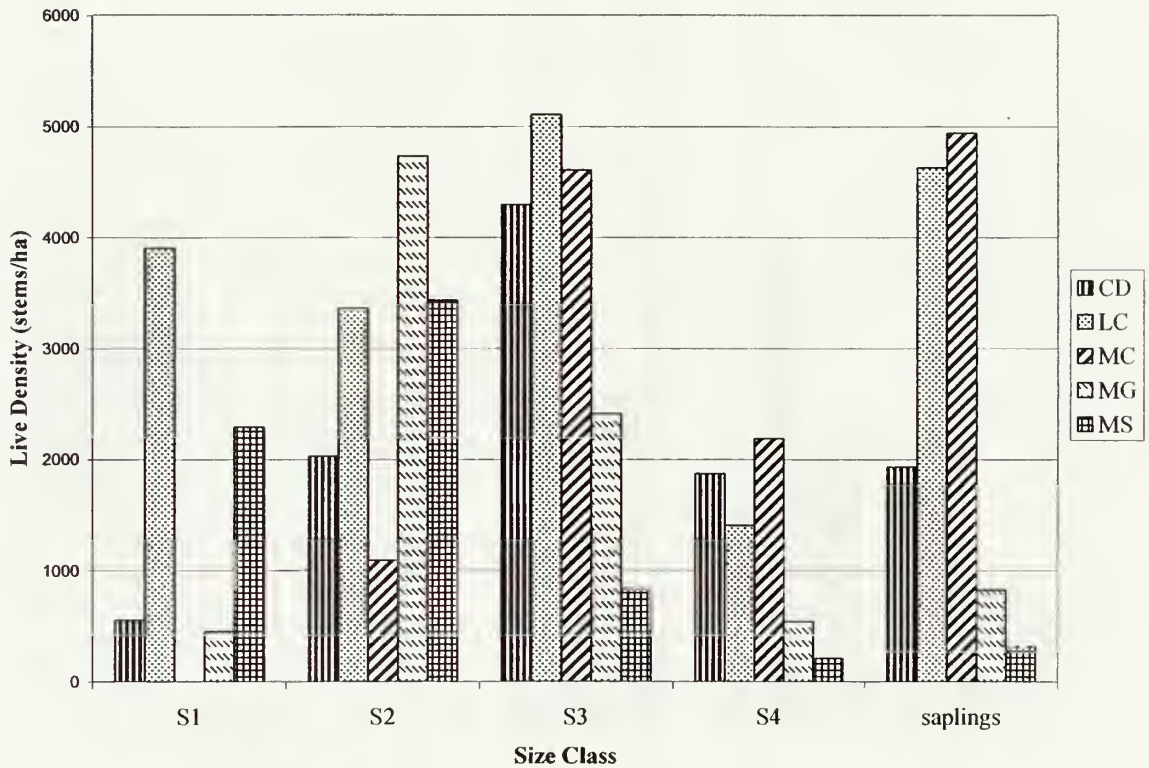


Figure 13. Mean densities (stems/ha) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) Fraser fir in 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

Mt. Sterling was the only peak to decrease in red spruce sapling density from 1990-91 to 2000 (79 stems/ha) (Table 19). Despite this decrease in saplings all of the seedling size classes increased in density (Table 19). Mt. Collins showed the greatest increase in spruce sapling density from 1990-91 to 2000 (stems/ha) (Table 19). This peak also exhibited the greatest reduction in spruce seedlings (25,313 stems/ha) (Table 19).

The only peak to increase in mountain-ash understory density was Mt. LeConte (13,223 stems/ha) (Table 20). Considering the low densities of the overstory and understory mountain-ash this is a relatively large increase. No mountain-ash understory stems were found on Mt. Sterling (Table 20). Similarly there were very few stems in 1990-91 probably due to the low elevation of this summit (Table 20). Mountain-ash has been shown to increase with increasing elevation (Ramseur 1960; Smith 1997).

Understory yellow birch was absent on Clingmans Dome in 1990-91 and 2000 (Table 21). Since Clingmans Dome was the highest summit low densities of yellow birch were expected. Ramseur (1960) observed fewer yellow birch stems with increasing elevation. This peak also had the lowest densities of overstory yellow birch.

The other hardwood understory density was highest on Mt. Sterling (833 stems/ha) (Table 22). This peak also held the highest density and basal area of other hardwoods overstory. Other studies have shown that these hardwoods decrease with increasing elevation (Crandall 1958).

The largest reduction of understory shrubs was found on Mt. Collins (5,528 stems/ha) (Table 23). Nevertheless, this peak held the greatest density of understory shrubs in 2000 (Table 23).

Table 19. Mean densities (stems/ha ± SD) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) red spruce in 1990-91 and 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

| Size Class | Mountain Peak | | | | | |
|---|---|---|---|---|---|---|
| | CD | | LC | | MC | |
| | 1990-91 | 2000 | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 6518 ± 7645 | 313 ± 668 | 6016 ± 9618 | 1719 ± 1969 | 7266 ± 11731 | 156 ± 289 |
| S2 | 12589 ± 18155 | 1250 ± 2339 | 6250 ± 12142 | 2109 ± 2968 | 17813 ± 28547 | 156 ± 289 |
| S3 | 536 ± 915 | 1797 ± 3033 | 2031 ± 3252 | 1641 ± 2499 | 1953 ± 2044 | 1172 ± 1130 |
| S4 | 89 ± 236 | 781 ± 1728 | 0 | 547 ± 1130 | 234 ± 465 | 469 ± 868 |
| All Seedlings | 19732 ± 25850 | 4141 ± 5966 | 14297 ± 24582 | 6016 ± 7402 | 27266 ± 41234 | 1953 ± 2349 |
| Saplings | 22 ± 59 | 273 ± 200 | 78 ± 167 | 371 ± 668 | 156 ± 277 | 664 ± 571 |
| Total Understory | 19754 ± 25830 | 4414 ± 6044 | 14375 ± 24746 | 6387 ± 7932 | 27422 ± 41187 | 2617 ± 2746 |

| Size Class | Mountain Peak | | | |
|---|---|---|---|---|
| | MG | | MS | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 982 ± 709 | 89 ± 236 | 0 | 521 ± 831 |
| S2 | 1696 ± 1830 | 1161 ± 2086 | 2292 ± 4754 | 2396 ± 5869 |
| S3 | 357 ± 709 | 179 ± 305 | 625 ± 791 | 1354 ± 2750 |
| S4 | 89 ± 236 | 446 ± 1181 | 0 | 104 ± 255 |
| All Seedlings | 3125 ± 3146 | 1875 ± 2818 | 2917 ± 5209 | 4375 ± 9512 |
| Saplings | 112 ± 118 | 424 ± 610 | 339 ± 554 | 260 ± 352 |
| Total Understory | 3237 ± 3235 | 2299 ± 3132 | 3255 ± 5191 | 4635 ± 9485 |

Table 20. Mean densities (stems/ha ± SD) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) mountain-ash in 1990-91 and 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

| Size Class | Mountain Peak | | | | | |
|---|---|---|---|---|---|---|
| | CD | | LC | | MC | |
| | 1990-91 | 2000 | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 982 ± 1133 | 313 ± 884 | 1797 ± 2940 | 16328 ± 35820 | 547 ± 1079 | 0 |
| S2 | 268 ± 492 | 0 | 1094 ± 1283 | 156 ± 442 | 0 | 0 |
| S3 | 179 ± 305 | 0 | 781 ± 1095 | 0 | 156 ± 289 | 0 |
| S4 | 0 | 0 | 0 | 78 ± 221 | 0 | 0 |
| All Seedlings | 1429 ± 1002 | 313 ± 884 | 3672 ± 3917 | 16563 ± 36204 | 703 ± 1313 | 0 |
| Saplings | 0 | 98 ± 143 | 117 ± 182 | 449 ± 1094 | 20 ± 55 | 98 ± 220 |
| Total Understory | 1429 ± 1002 | 410 ± 978 | 3789 ± 4050 | 17012 ± 35993 | 723 ± 1302 | 98 ± 220 |

| Size Class | Mountain Peak | | | |
|---|---|---|---|---|
| | MG | | MS | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1250 ± 2009 | 268 ± 709 | 0 | 0 |
| S2 | 982 ± 1189 | 357 ± 610 | 104 ± 255 | 0 |
| S3 | 446 ± 783 | 0 | 0 | 0 |
| S4 | 179 ± 472 | 179 ± 472 | 0 | 0 |
| All Seedlings | 2857 ± 3588 | 804 ± 1642 | 104 ± 255 | 0 |
| Saplings | 22 ± 59 | 134 ± 190 | 0 | 0 |
| Total Understory | 2879 ± 3577 | 938 ± 1685 | 104 ± 255 | 0 |

Table 21. Mean densities (stems/ha ± SD) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) yellow birch in 1990-91 and 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

| Size Class | Mountain Peak | | | | | |
|---|---|---|---|---|---|---|
| | CD | | LC | | MC | |
| | 1990-91 | 2000 | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 0 | 0 | 781 ± 801 | 0 | 1484 ± 2754 | 0 |
| S2 | 0 | 0 | 156 ± 289 | 0 | 0 | 0 |
| S3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S4 | 0 | 0 | 0 | 0 | 0 | 0 |
| All Seedlings | 0 | 0 | 938 ± 945 | 0 | 1484 ± 2754 | 0 |
| Saplings | 0 | 0 | 0 | 176 ± 328 | 39 ± 72 | 39 ± 72 |
| Total Understory | 0 | 0 | 938 ± 945 | 176 ± 328 | 1523 ± 2751 | 39 ± 72 |

| Size Class | Mountain Peak | | | |
|---|---|---|---|---|
| | MG | | MS | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 268 ± 334 | 0 | 4375 ± 8506 | 0 |
| S2 | 89 ± 236 | 0 | 104 ± 255 | 0 |
| S3 | 89 ± 236 | 0 | 0 | 0 |
| S4 | 0 | 0 | 0 | 0 |
| All Seedlings | 446 ± 695 | 0 | 4479 ± 8754 | 0 |
| Saplings | 0 | 22 ± 59 | 104 ± 128 | 26 ± 64 |
| Total Understory | 446 ± 695 | 22 ± 59 | 4583 ± 8864 | 26 ± 64 |

Table 22. Mean densities (stems/ha ± SD) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) other hardwood class in 1990-91 and 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

| Size Class | Mountain Peak | | | | | |
|---|---|---|---|---|---|---|
| | CD | | LC | | MC | |
| | 1990-91 | 2000 | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 0 | 0 | 1719 ± 2270 | 0 | 625 ± 1294 | 0 |
| S2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S3 | 0 | 0 | 0 | 0 | 156 ± 442 | 78 ± 221 |
| S4 | 0 | 0 | 0 | 0 | 78 ± 221 | 78 ± 221 |
| All Seedlings | 0 | 0 | 1719 ± 2770 | 0 | 859 ± 1334 | 156 ± 289 |
| Saplings | 0 | 0 | 0 | 39 ± 72 | 254 ± 602 | 176 ± 437 |
| Total Understory | 0 | 0 | 1719 ± 2770 | 39 ± 72 | 1113 ± 1601 | 332 ± 681 |

| Size Class | Mountain Peak | | | |
|---|---|---|---|---|
| | MG | | MS | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 0 | 0 | 0 | 729 ± 1786 |
| S2 | 0 | 0 | 833 ± 1461 | 104 ± 255 |
| S3 | 0 | 0 | 313 ± 765 | 0 |
| S4 | 0 | 0 | 0 | 0 |
| All Seedlings | 0 | 0 | 1146 ± 1602 | 833 ± 2041 |
| Saplings | 134 ± 355 | 0 | 208 ± 323 | 0 |
| Total Understory | 134 ± 355 | 0 | 1354 ± 1650 | 833 ± 2041 |

Table 23. Mean densities (stems/ha ± SD) of live seedling (S1-unbranched, S2-branched ≤.25 m, S3-.26 m-1.0m tall, S4-1.01 m - 1.36 m tall) and sapling (≥1.37 m tall, >5 cm dbh) shrubs in 1990-91 and 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

| Size Class | Mountain Peak | | | | | |
|---|---|---|---|---|---|---|
| | CD | | LC | | MC | |
| | 1990-91 | 2000 | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 1071 ± 935 | 156 ± 442 | 859 ± 880 | 0 | 391 ± 465 | 2656 ± 4075 |
| S2 | 0 | 78 ± 221 | 469 ± 647 | 0 | 0 | 859 ± 1247 |
| S3 | 6875 ± 5830 | 703 ± 779 | 625 ± 747 | 234 ± 663 | 11016 ± 9642 | 3281 ± 3594 |
| S4 | 1250 ± 1614 | 703 ± 911 | 0 | 0 | 2734 ± 2853 | 1094 ± 1407 |
| All Seedlings | 9196 ± 7567 | 1641 ± 1635 | 1953 ± 1782 | 234 ± 663 | 14141 ± 12703 | 7891 ± 9384 |
| Saplings | 2278 ± 2854 | 1231 ± 1389 | 781 ± 1851 | 274 ± 565 | 2207 ± 2552 | 2930 ± 2195 |
| Total Understory | 11473 ± 9849 | 2871 ± 2238 | 2734 ± 2706 | 508 ± 1204 | 16348 ± 15152 | 10820 ± 11333 |

| Size Class | Mountain Peak | | | |
|---|---|---|---|---|
| | MG | | MS | |
| | 1990-91 | 2000 | 1990-91 | 2000 |
| S1 | 0 | 0 | 0 | 0 |
| S2 | 625 ± 1398 | 0 | 104 ± 255 | 104 ± 255 |
| S3 | 1250 ± 3041 | 0 | 313 ± 523 | 104 ± 255 |
| S4 | 179 ± 472 | 0 | 313 ± 765 | 0 |
| All Seedlings | 2054 ± 4891 | 0 | 729 ± 1501 | 208 ± 323 |
| Saplings | 938 ± 2345 | 603 ± 1527 | 599 ± 1467 | 443 ± 1084 |
| Total Understory | 2991 ± 7230 | 603 ± 1527 | 1328 ± 2063 | 651 ± 1312 |

### 5.2.4. Herbaceous Layer

The percentage of ground covered by the herbaceous layer largely decreased on all mountain peaks from 1990-91-200. By stand type all but the PLF type decreased in herbaceous cover. Overall the herbaceous cover decreased by 38%. This can be attributed to competition for light and space from a large increase in sapling density of all species combined (Table 9).

Among the most common herbaceous plants in order of abundance were ferns (*Dryopteris* sp.), thornless blackberry, wood sorrel, asters, bearberry, various species of carrex, bluebead-lilly (*Clintonia borealis* (Aiton) Raf.), and various species of grass. Before the arrival of the adelgid, Ramseur (1960) also noted that the ferns were the most dominant species in the herbaceous layer.

## 5.3. Age Distribution of Fraser Fir

### 5.3.1. Overall

Pre adelgid infestation, Oostings and Billings (1951) found the average maximum age of fir in the Great Smoky Mountains to be 150 years. Naturally, from the 1940s to 1990, the disturbance caused by the adelgid caused the spruce-fir overstory to decrease in age structure. There was also a decrease in age from 1990-91 to 2000 (58 and 36 years respectively) (Table 11). However, this should be viewed skeptically, because in 1990-91 there were no trees cored in the dead fir stand types. Nonetheless the general trend in the overstory shifted from primary to secondary growth. There were significant decreases in the mean ages of the S1, S4, and sapling size classes (Table 11). These decreases show an increase in vigor in

an increase in vigor in response to the extra available light reaching the understory following the adelgid caused disturbance.

### 5.3.3. By Stand Types

The MLF type had the largest mean age of the overstory fir sampled in 1990-91 and 2000 (64.9 and 43.9 years respectively) (Figure 14, Figure 15). The spread of mean ages of overstory fir among stand types ranged from 31.6 years in the PDF and 43.9 years in the MLF.

The MDF type had the highest mean age in the sapling size class (22 years) (Figure 15). The oldest mean age of fir in the S1 size class was in the MDF type (4.1 years). In the S2 size class the highest mean age was 10.9 years, in the MLF. The MDF type had the highest mean age for the S3 size class (15.6 years), and the MDF has the highest mean age for the S4 size class (17.9 years).

### 5.3.4. By Mountain

The mean ages of overstory fir ranged from 33 years on Mt. Steerling to 43 years on Clingmans Dome (Figure 16). This was small range in ages compared to the 38 year gap in 1990-91 between Mt. Sterling and Mt. Collins (Figure 17).

The understory fir ages did not resemble the same trend as the overstory fir between peaks (Figure 16). Mount Collins had the highest mean age of all the understory size classes except the S3 size class which was highest on Mt. Sterling.

### 5.4. Foliage Chemistry

The 2000 and 2001 foliage were analyzed for phosphorous, potassium, calcium, magnesium, copper, iron, manganese, zinc, and aluminum (Table 24). Elements K and Cu were left out because of suspect contamination. These data will be used for future comparative analysis.

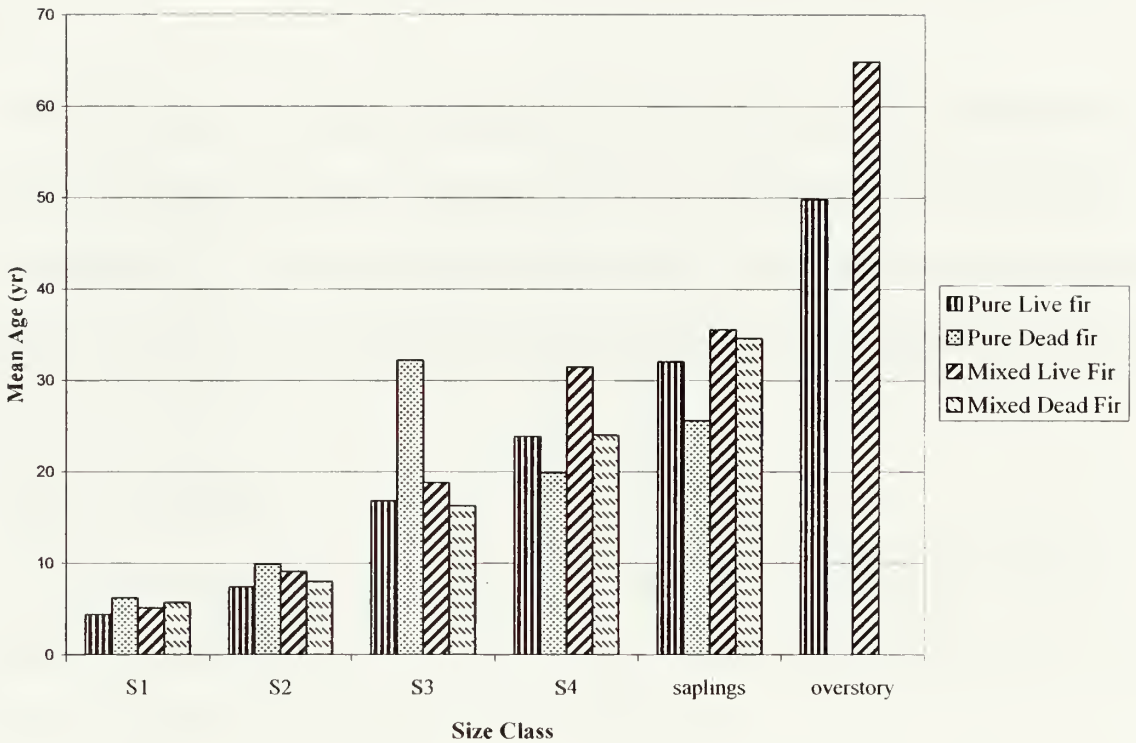


Figure 14. Mean ages (yr) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)), sapling (≥1.37 m tall, and <5 cm dbh), and overstory (≥5 cm dbh) Fraser fir in 1990-91 in all stand types (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

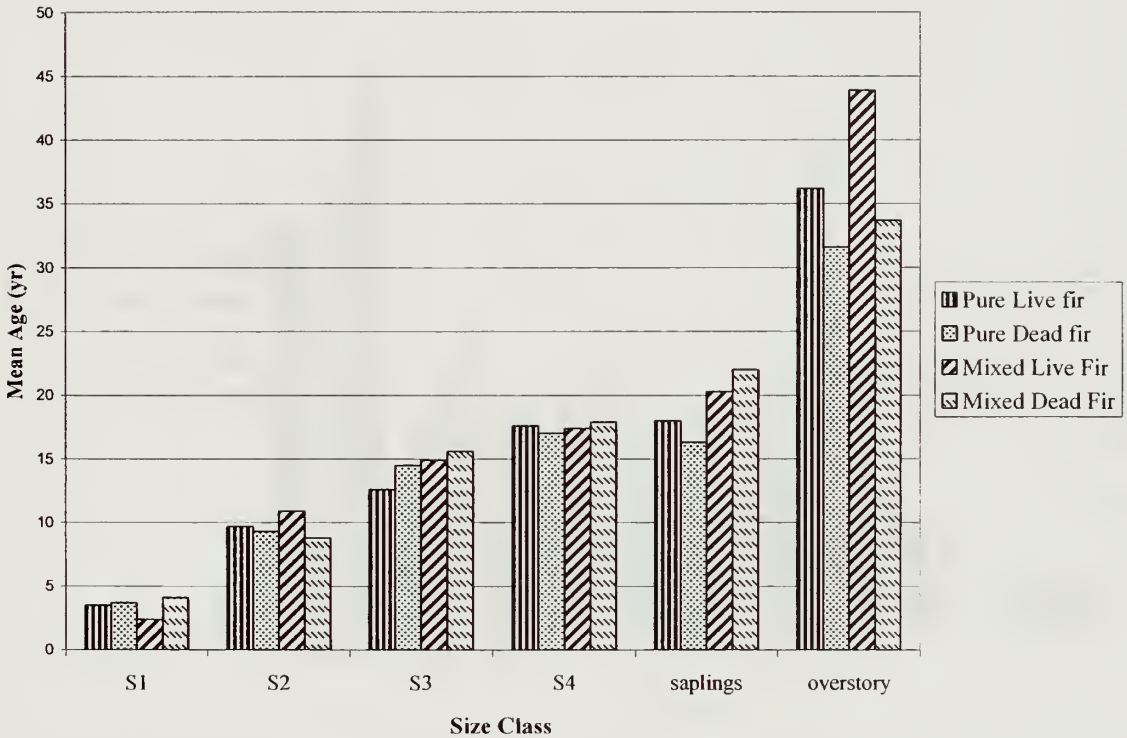


Figure 15. Mean ages (yr) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)), sapling (≥1.37 m tall, and <5 cm dbh), and overstory (≥5 cm dbh) Fraser fir in 2000 in all stand types (PLF-pure live fir, PDF-pure dead fir, MLF-mixed live fir, MDF-mixed dead fir).

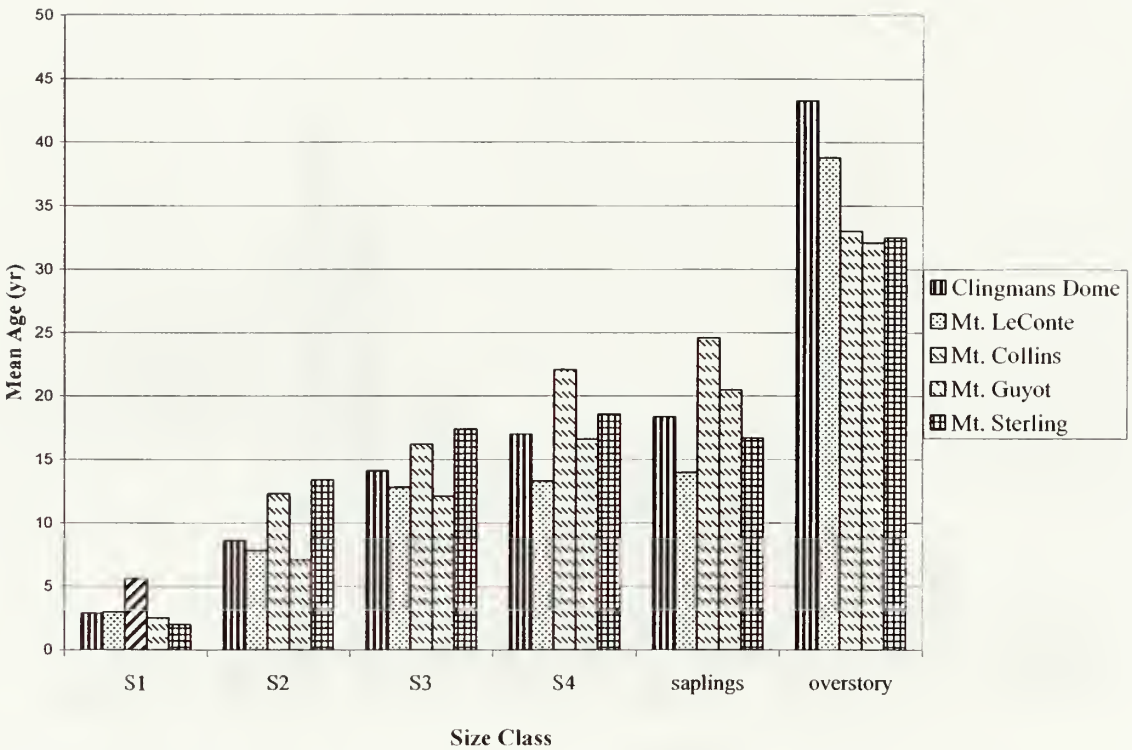


Figure 16. Mean ages (yr) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)), sapling (≥1.37 m tall, and <5 cm dbh), and overstory (≥5 cm dbh) Fraser fir in 2000 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

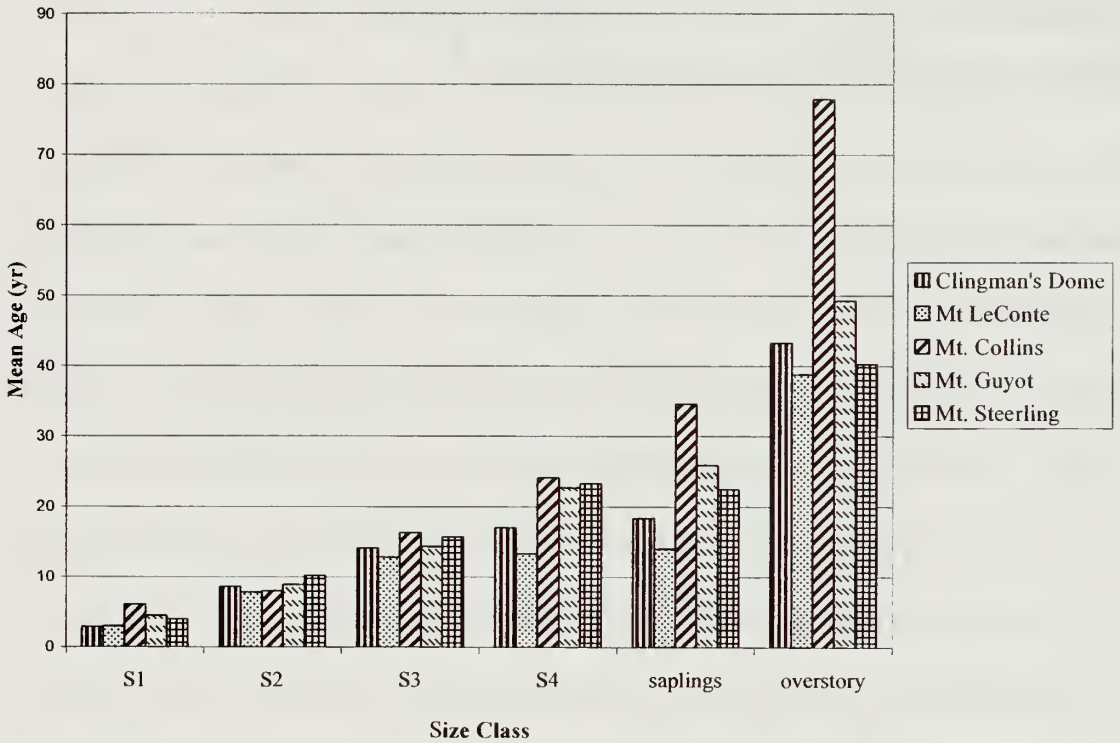


Figure 17. Mean ages (yr) of live seedling (1-4 years (S1), 4 years-.25 m tall (S2), .26 m-1.0 m tall (S3), and 1.01-1.36 m tall (S4)), sapling (≥1.37 m tall, and <5 cm dbh), and overstory (≥5 cm dbh) Fraser fir in 1990-91 on five mountain peaks (CD-Clingmans Dome, LC-Mount LeConte, MC-Mount Collins, MG-Mount Guyot, MS-Mount Sterling).

Table 24. Foliage chemistry of new growth (2001) and previous year's growth (2000) Fraser fir.

| Element | Previous Year's Growth | New Growth |
|---|---|---|
| **P %** | 13.39% | 23.98% |
| **Ca %** | 30.69% | 14.19% |
| **Mg %** | 7.08% | 7.47% |
| **Fe (mg/kg)** | 52.92 | 46.09 |
| **Mn (mg/kg)** | 737.39 | 331.99 |
| **Zn (mg/kg)** | 24.93 | 32.87 |
| **Al (mg/kg)** | 186.65 | 189.16 |

## CONCLUSIONS

The southern Appalachian red spruce-Fraser fir ecosystem has been subjected to significant levels of stress over the past century impacting the structure and composition of the forest. Values of spruce and fir basal areas and densities were dramatically lower in 1990-91 than found in the late 1940s (pre balsam woolly adelgid infestation). Between 1990-91 to 2000, however, the live overstory fir density increased by 156 stems/ha. Despite this increase in density, the new cohort remained sparse compared to pre-adelgid conditions. The spruce component suffered losses in basal area from the 1940s to 1990, probably due to "thinning shock" created from exposure to wind, light, and temperature fluctuations. There were no losses in spruce basal area and density from 1990-2000 because of an increased fir component lessening the negative effects of wind exposure.

Mortality rates decreased for all major species groups since the late 1980s. The decrease in fir mortality was the result of the reduction in the larger older more susceptible fir prior to this study, leaving behind a sparse cohort of younger more resistant trees. The decrease in spruce mortality can be explained by the declining negative effects of "thinning shock" caused by exposure. Mountain-ash mortality probably decreased from less impact caused by the mountain-ash sawfly, and an increased vigor due to a surplus of available light.

Overall there was a decrease in the seedling cohort. Two possibilities explain the decrease in fir seedlings: 1) competition for space from the sapling layer or 2) difficulty in seed germination caused by soil dessication. The spruce seedlings decreased from three possible factors: 1) competition for space from the saplings 2) voids between large seed

crop years (3-8 years (Hart 1965)) or 3) low soil moisture caused from increased sunlight. Nevertheless, mountain-ash seedlings increased. This increase in mountain-ash seedlings is probably the result of this shade intolerant species thriving in response to the increased sunlight made available from the overstory deterioration.

The mean ages of fir sapling, S1, and S4 size classes decreased significantly since 1990-91. This indicates a vigorous rapidly growing understory in response to overstory change. This increase in vigor was also noted by Smith and Nicholas (2000) who suggested that young fir was rapidly replacing the overstory as a result of greater canopy openness

Whether this dense rapidly growing fir understory will resemble the uneven-aged forest that existed prior to the balsam woolly adelgid infestation remains unknown. If the fir does not develop a resistance and adelgid populations do not stabilize it is possible that once this cohort reaches maturity the balsam woolly adelgid could have another explosive outbreak completely replacing the overstory. Provided this cohort reaches seed bearing age, the spruce-fir will remain a two-aged forest never obtaining an uneven-aged structure. Prior to adelgid infestation, red spruce often lived more than 300 years while fir reached a maximum age around 150 years (Korstian 1937). This "old growth" fir and spruce will likely no longer be a part of this ecosystem. However, if the adelgid populations stabilize or the Fraser fir develop a resistance to the insect the forest could possibly achieve an "old growth" uneven-aged structure similar to what existed prior to infestation.

## 6. SUMMARY CONCLUSION:

Although the understory Fraser fir appears dense and vigorous the future of this new cohort of trees is unknown. One possibility is a sudden demise. Provided the adelgid population does not stabilize, or Fraser fir does not develop a resistance, a thick even-aged stand of fir may trigger another large population outbreak in adelgids causing even higher numbers of fir mortality than the initial infestation. This may result in a forest of reduced size trees that barely reach cone bearing age before they are killed by the adelgid. Another scenario is adelgid population stabilization, or a developed resistance of Fraser fir trees. In this case it is possible the forest could obtain the "old growth" uneven-aged structure similar to what existed prior to infestation.

## 7. RECOMMENDATIONS

1) The thirty-seven plots should be revisited every ten years and monitored for change. Close attention should be paid to the success of the newly established cohort of trees; Are they producing cones? Does the impact of the adelgid on this second generation of trees cause as much mortality as the initial outbreak? Also the success of understory establishment should be monitored to determine if viable seed is still being produced.

2) The GSMNP should continue to keep the public informed of the impact of the balsam woolly adelgid on the spruce-fir forest. The aesthetic value of seeing the forest of fir snags on Clingmans Dome should be used to enforce the idea that introduced exotics can cause catastrophic disturbances in a natural area. Also the new growth is a good tool to illustrate the concept of succession. Increased public awareness of the problems in the spruce-fir forests would decrease the chances of something similar happening in the future.

3) The stand type designation was determined to be obsolete and should be discarded from the study.

## 8. METHODOLOGY IMPROVEMENTS AND SUGGESTED CHANGES

**1.** Some quality control is needed. At least one of the plots should be sampled twice by two different groups of data collectors. This will assure that the methodology and subjective observations are consistent among the data collectors. This should be done early in the season to correct any problems and inconsistencies that may arise.

**2.** At the top of each data collection page the full date and names of each data collector involved must be written. If a problem arises in the data analysis step it is important to isolate any bias that might exist.

**3.** Try to sample the plots consistently at the same time of year that they were previously sampled. This is especially important with the herbaceous sampling because certain species germinate and bloom at different times of year.

**4.** When selecting trees to core use random tree numbers rather than selecting the largest trees in the plot.

**5.** Use straws to store the tree cores. When returning to the lab freeze, mount, and dye them to make ring counting more precise.

**6.** When collecting samples such as bark, root, tree cores, and soil, use detailed field cards with the protocol written on them. Be as specific as possible.

## 9. ACKNOWLEDGEMENTS

We would like to acknowledge certain people for their guidance and hard work on this report. Krisine Johnson, who through the support of the National Park Service, funded and initiated this project. Scott Kichman, who through all types of inclement weather, led the hard working 2000 summer field crew. We would also like to thank each crew member of the 2000 and 2001 field crew ; N. Bibis, M. Burton, C. Cordell, P. Craig, K. Culbertson, J. Diaz, J. Dumyahan, J. Eikenberry, K. Gillman, P. Hadala, M. Kloster, K. Mancusi, P. Petersen, L. Sprow, L. Tanner, G. Taylor, E. Worthington, and M. Wood. Additionally we would like to thank the 1990 and 1991 field technicians; D. Awl, P. Durr, E. Pauley, S. Pilsk, L. Renfro, and L. Richmond. Finally we would like to thank George Smith who did the initial data analysis and report writing with the data collected in 1990 and 1991. It was very helpful to have his work to use as a reference when writing this report.

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...Mountains...

r'ir Forest (1990-2000)

Appendix 1

Fraser fir assessment data sets